

6.1 Modern Case Study: Forest-Farmland Pitfall Trap Transects in Lammi, Finland

Primary reference: Koivula *et al.* (2004).

6.1.1 Aims

Koivula *et al.* undertook a pitfall trapping project to investigate the carabid (ground beetle) communities on eight transects running from forest into farmland environments in the Lammi area of southern Finland (61°03'–61°08'N, 24°55'–25°05'E). They examined the frequency of species at different distances into each habitat, and discussed the implications of these findings with respect to a variety of habitat related traits for the species found. Their catch results, with species classified in three habitat groups, are presented in Figure 6.2, and are compared with the environmental reconstruction outputs produced by the BugsCEP component BugStats. The aim here is to assess the ability of the different BugStats calculation methods to reconstruct the modern habitats sampled in the original paper.

6.1.2 Introduction

Modern studies which use Coleoptera to examine environmental changes are, in principal, the same as those which reconstruct past environments. There are different taphonomic and identification problems, and the sampling methods are quite unlike, but the result is a set of species abundances from a number of sample points. Both studies require that the habitat preferences and environmental tolerances of the species identified are known. There is, however, a major difference in that modern studies have the definite potential to contribute to the understanding of the ecology of the species found, whereas fossil studies ultimately rely on other modern studies and can, perhaps, only contribute to modern ecology in terms of increasing the understanding the past biogeography of the species.

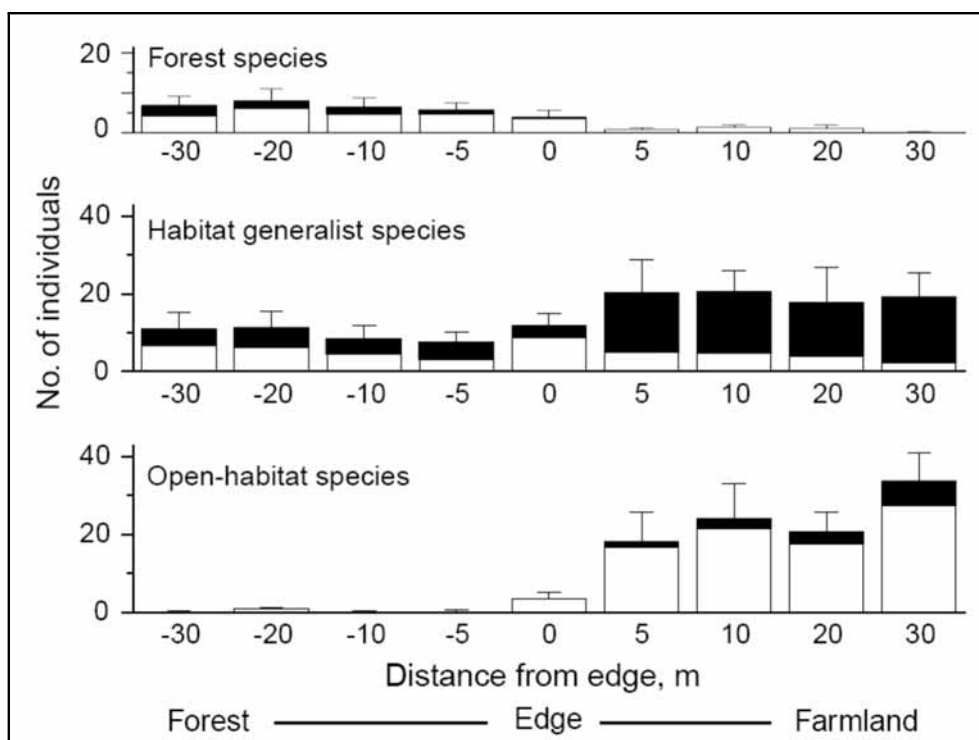


Figure 6.2. Mean adjusted catch (and SE) of carabids of three habitat groups along forest - farmland transects. Black/white shading represents different trapping episodes. Note that the Forest species y-axis has been rescaled in this thesis to match the other habitat scales. [Reproduced with permission from Koivula *et al.* (2004)].

Although designed primarily for assisting the study of past environments, the BugStats system can only be shown to be robust if it works for modern assemblages. It is, after all, built on the modern understanding of species habitat preferences. This case study tests that hypothesis for a small test set.

6.1.3 Methods

Koivula et al. (2004) methods:

Fifty nine carabid species were collected from a total of 288 pitfall traps along eight forest-farmland transects, as described in Table 6.1. Collection was undertaken in two periods between 24th May and 15th August 2001. Species were classified “...according to their coarse habitat association...” (*ibid.* p299) into Forest, Generalist, and Open habitat species. This is much the same method as used in the Bugs EcoCode classification system, although the information sources used vary somewhatⁱ, and BugsCEP includes a larger number of classes. Catch frequencies were adjusted to compensate for lost traps (mean no. of individual/trap x 20 days), and the grouped classifications presented as plots against the trap distances from the forest-farmland edge (Figure 6.2). The two most common species in each habitat class were: Forest: *Calathus micropterus* (Dft.) and *Pterost. Oblongopunctatus* (F.); Generalist: *Pterostichus melanarius* (Ill.) and *Pterostichus niger* (Schall.); Open: *Amara montivaga* Sturm and *Carabus cancellatus* Ill.; a full list can be found in the appendix of Koivula *et al.* (2004). Koivula *et al.* also undertook a number of statistical analyses (including ANOVA and DCA) in order to try to understand the response of different groups of carabid species to variations in the habitats sampled. These analyses will not be discussed here, but their conclusions will be referred to where relevant.

Table 6.1. Sampled landscape units summarized from Koivula *et al.* (2004)

Landscape unit	Description
Forest	<i>Oxalis-Myrtillus</i> -type mesic mixed-wood forests, dominated by Norway spruce (<i>Picea abies</i>), birches (<i>Betula</i> spp.) and aspen (<i>Populus tremula</i>). The age of the dominant trees was 80–120 years.
Farmland	Five grass (<i>Trifolium</i> and <i>Taraxacum</i>) dominated hay meadows; Two set-aside plots ((<i>Trifolium</i> and <i>Taraxacum</i> plus <i>Stellaria media</i>); One crop field (bare ground and wheat (<i>Triticum</i>) in respective sampling periods).

BugsCEP methods:

As the raw pitfall trap data were not published, three pseudo-samples were created to contain the grouped trap total abundance values. Koivula *et al.* provided total catch values for each species, and percentage catch values for three trap groups based on distance from the forest-farmland edge (Koivula *et al.* 2004: p307 - Appendix) as follows:

Forest: traps 10-30 m from edge

Edge: traps ± 5 m from the edge

Farmland: traps 10-30 m from edge

The adjusted catch percentage values were converted to approximate raw abundance values to enable abundance weighting in the calculations, and imported into BugsCEP as a countsheet attached to a new site. The BugStats EcoFig routine was run on this data with several calculation combinations. A standard BugsCEP full site report and species-EcoCode breakdown report are included in the digital appendix of this thesis for further reference. Detailed explanations of the calculations involved in the construction of Bugs EcoFigs can be found in Chapter 4, and will therefore only be summarized here:

ⁱ See the ‘Lammi’ digital appendix data on the CD accompanying this thesis for full details.

- Abundance weighted – the EcoCodes for each species are multiplied by the species sample abundance.
- Species presence only – the EcoCodes for each species are only counted once for each habitat class (also referred to as *no abundance*).
- Raw – count data are presented without standardization.
- %SumRep – count data for each habitat class are given as a percentage of the sum of the count data for all classes. These diagrams are more viable for inter-site comparisons.
- $\ln(n+1)$ – count data (+1) is natural logarithm transformed. This is done after abundance weighting and before applying %SumRep standardization, and can help compensate for skewed population distributions. (Note that Koivula *et al.* used the same transformation before performing ANOVA and DCA analyses on the data).

A species may represent more than one habitat class, and so abundance and NSpec (species richness) totals are not the same as the sum of environmental representation counts (SumRep) for each sample.

Eight different Bug EcoFigs can be created for data with species level identifications, six of which are presented here. $\ln(n+1)$ transformed ‘species presence only’ diagrams have been omitted as they are more informative of the degree of habitat specialization of the species involved, and of the code designation system itself, than of the environments represented by the species. The diagrams used collectively present different possibilities for the reconstruction of the environment from the list of beetles found in each trapping zone. Variations in the species compositions of each zone, when which are processed in the construction of each diagram, transform the habitat information in the data to signals of different relative strengths, which must be interpreted with care.

A BugsMCR thermal reconstruction was run on the data for the sake of experimentation, and as a further validation of the MCR dataset. The results are presented in Table 6.3.

6.1.4 Results and preliminary discussion

On first examination, none of the BugStats outputs (Figure 6.3) seem to illustrate the difference between the three habitat-association groups as clearly as the diagram presented in Koivula *et al.* (Figure 6.2). As the latter is from mean adjusted catches, one would expect the raw abundance weighted BugStats diagram to be most comparable (Figure 6.3b). This appears to be the case when comparing Koivula *et al.*’s Farmland with the Bugs EcoCode categories *Disturbed/arable* and *Sandy/dry disturbed/arable*ⁱⁱ, with the BugStats output practically mirroring the pattern created by the average of the transect traps. The drier nature of the farmland is clearly evident in the *Sandy/dry disturbed/arable* graph. *Heathland & moorland*, and *Meadowland* species are also more strongly represented in the Farmland traps. *Wood & trees*, however, is not clearly differentiated between the samples in this diagram (Figure 6.3b). However, the *Wetland/marshes* signal is stronger in the Forest sample, as would be expected, given the generally higher humidity and soil moisture usual in forest environments (Geiger *et al.*, 2003). A casual glance at the *Abundance* and *SumRep* graphs suggests that this could be due to the far greater abundance in the farmland traps, which is reflected in the sample sum of represented environments (SumRep) when using abundance weighting. In this case, the arable land tends to support both higher numbers of carabid individuals and species than woodlands, although this should be expected to vary with the nature of the substrate. It should also be noted that this is reflected in the number of carabid species respectively classed in BugsCEP as *Wood & trees* (82) and *Disturbed/arable* or *Sandy/dry disturbed/arable* (105). General ecological knowledge also tells us that ecotones (Edge) and disturbed environments have higher expected species richness than stable environments (Colinvaux, 1973). Although the Edge samples had higher species richness than the stable Forest environment, it was lower than the Farmland, suggesting that the effect of farmland disturbance on species richness is stronger than the ecotone (Edge) effect. This lends more support for the standardization of EcoCode graph values to enable inter-sample comparison.

ⁱⁱ BugStats classifications will be given *italicised* to avoid confusion.

By using the ‘%SumRep’ options in BugStats, graph values can be recalculated as percentages of the total sums of representations for each sample, thus compensating for differences in sample abundances (or species richness when abundance weighting is not used). When weighted abundance values are applied, the *Wood & trees* signal appears much more prominent (Figure 6.3a). A clear gradient can be seen in its drop through Edge to Farmland samples, and in addition, the soil moisture indicative classes *Meadowland* and *Wetland/marshes* give a stronger signal in the Forest traps. The two *arable* BugStats classes undergo little change except for the increase of the *Disturbed/arable* signal in the Edge sample with respect to the Farmland sample. It may be interesting to note that *Heathland/moorland* species are represented equally in the Forest and Farmland samples, and only slightly less in the Edge sample. This could either reflect a tendency in heathland Carabidae to be less habitat specific; be a reflection of the broad definition of the terms in the literature upon which the Bugs EcoCodes designations are based; the nature of the ground flora or substrate in the woodland; or be a product of the classification system.

Although the use of %SumRep standardization on the abundance weighted data increases the visibility of some expected habitat signals, it can be seen from the remaining diagrams that some information is missing. In particular, Figure 6.3a and Figure 6.3b do not show any indication of *Open wet habitats* or *Halotolerant* species (i.e. salt enriched environments), but the remaining four diagrams show a small signal. Before discussing the significance of the signals themselves, their variable visibility should be explained. Log transforming species abundancesⁱⁱⁱ is a well known tool for normalizing population distributions in both ecology (Jongman *et al.*, 1995; Krebs, 1989; Southwood, 1978) and palaeoecology (e.g. Hammer & Harper, 2006; Kenward, 1978). This reduces the positive tail common in beetle assemblages, and may help to give the population distribution a more symmetrical (normal) form that is a prerequisite for a variety of statistical methods (e.g. regression, ANOVA). In abundance weighted diagrams it also reduces the significance of high abundance species and raises that of the rare species. This is reflected in the BugStats output by a reduction in the relative difference between the highest and lowest values, effectively flattening the diagram components. By comparing Figure 6.3b and Figure 6.3d, we can see that although the aforementioned small magnitude signals are revealed, the visible difference amongst the higher magnitude signals is apparently reduced – making differentiation of the three habitat groups difficult from the diagram. In this case the transformation was not useful, and this may be the case for many sites; BugStats was designed to work with non-transformed abundance or species presence data.

The ‘Species presence only’ diagrams are, in this case, more useful than the log transformed ones. In order to create these, BugStats has ignored all abundance data and only looked at the presence(/absence) of species, effectively reducing the significance of super-abundant species and increasing that of rare species. This may help compensate for differential susceptibility of species to trapping methods, or differential taphonomic loss of fossils. In some respects, it has a similar effect to log transformation, but tends to preserve more of the habitat characteristics of sample values – especially when %SumRep standardized, as can be seen in Figure 6.3e. It is good practice to present both abundance weighted (cf. number of individuals) and non-abundance weighted (species presence/cf. number of taxa) results to give a fuller picture of the population structure (e.g. Ponel 1995).

ⁱⁱⁱ $\ln(\text{abundance}+1)$ is used rather than $\ln(\text{abundance})$ due to the presence of zero values in most datasets.

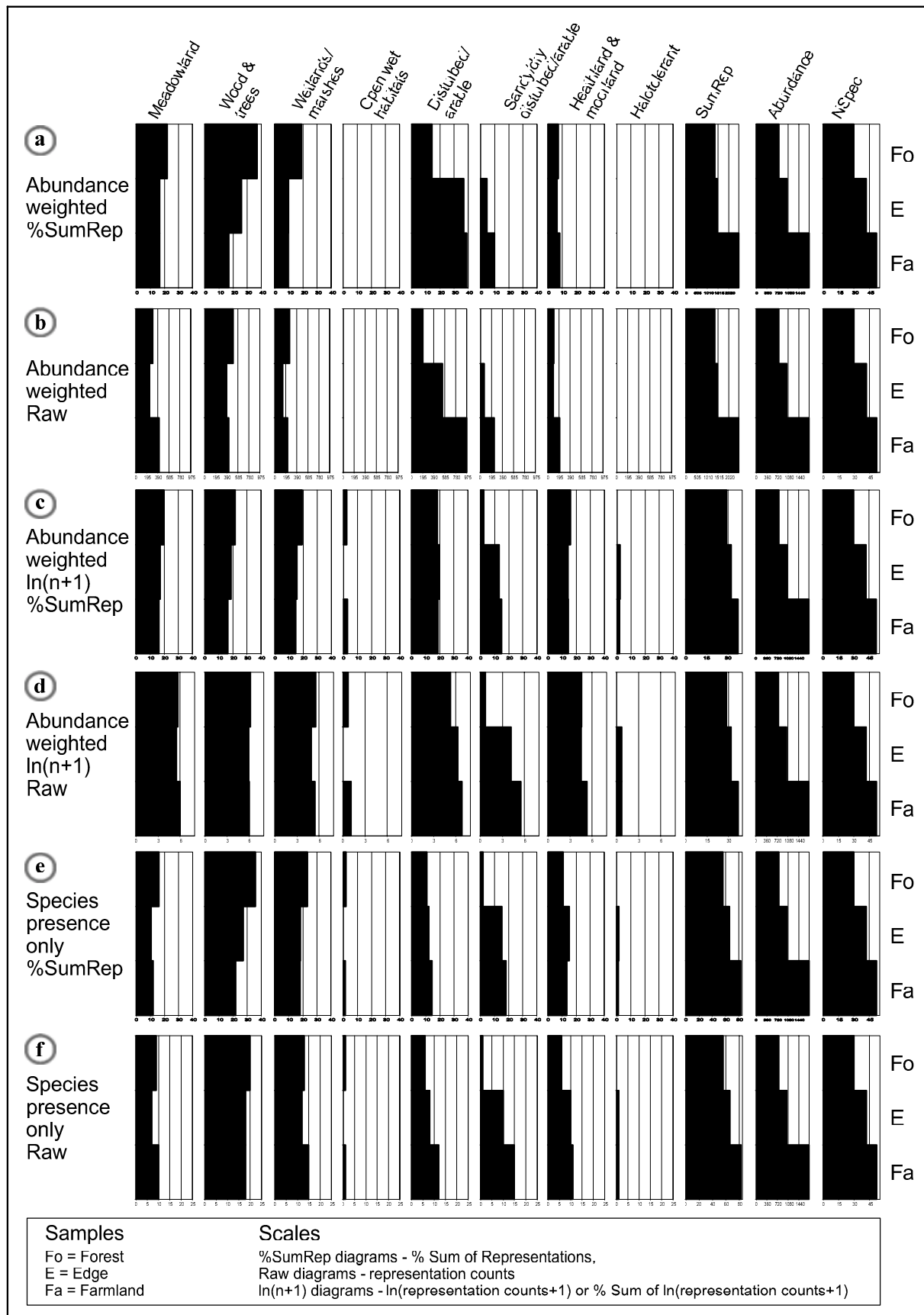


Figure 6.3. BugStats EcoFig output (edited) for Koivula *et al.* (2004) reconstructed grouped trap data. See text for discussion of variations. Note that the x-axes are different for each raw diagram. NSpec = Number of species.

Open wet habitats are to be expected in small forest openings, along stream banks or by pools and dew ponds in arable land. In this case, the signal is generated by a single occurrence of *Asaphidion flavipes* (L.) in the Forest, and two individuals of *Pterostichus vernalis* (Panz.) in the Farmland. *A. flavipes* is a eurytopic but hygrophilous species which prefers open environments (Koch, 1989; Lindroth, 1985), and is most probably an accidental presence in the Forest environment. *P. vernalis*, on the other hand, is a stenotopic, hygrophilous species common in moist areas of a range of environments (Koch, 1989; Lindroth, 1974; Luff, 1998), and so may indeed reflect a real, but small, microhabitat in the Farmland. *Halotolerant* species are most common in saline environments such as the shores of brackish water bodies, but may also be found in situations where high evaporation or erosion, be it natural or anthropogenic, increases the level of salts in the topsoil. They are therefore often present in arable landscapes, as ploughing mixes raw sediment with the upper organic soil horizons. *Halotolerant* species are totally absent from the Forest samples, and closer inspection of the fauna shows that one individual of the often coastal *Amara tibialis* (Payk.) (Koch, 1989; Luff, 1998) represents this habitat group in the Edge and Farmland samples. The *Halotolerant* habitat class should, however, be interpreted with care, as the reliability of the designation of a number of often coastal species is debatable and in need of revision.

Many authors (e.g. Kenward, 1978) often choose to exclude species with abundances lower than a certain threshold from analyses. This reduces the risk of casual occurrences affecting the results, but also risks filtering out small indicator and microhabitat signals that could contribute valuable information to an investigation. Such small scale indicators may or may not be important, and their usefulness will depend on the aims of the project^{iv}. A number of species are commonly only found in low frequencies (Colinvaux, 1973), and such filters potentially remove their input, and so should be applied carefully, with careful reflection on the sampling method.

Koivula *et al.* found that the Edge fauna was more similar to the Farmland fauna than the Forest Fauna, and the BugStats coefficient of similarity output supports this (Table 6.2).

Table 6.2. Modified Sørensen's coefficient of similarity (Southwood, 1978), showing slightly closer similarity between the Edge fauna and the Farmland fauna, than the Edge fauna and the Forest fauna^v.

	Forest	Edge	Farmland
Forest			
Edge	0.517165		
Farmland	0.300628	0.66289	

The MCR thermal reconstructions produced results comparable to the current central-southern Finnish climate (Table 6.3). A number points are of particular interest:

1. The reconstructions show a slightly wider TValue span in the Forest than in the other habitats, and indicate a slightly more continental climate in its TRange span. This has implications for the use of MCR with fossil material, in that the past environment must be reconstructed in terms of its habitats whenever calculating MCR, so that such factors can be reconsidered. It can be suggested, from the results of this study, that reconstructed winter temperatures are more sensitive to differences in the habitat preferences of the species used for reconstruction, although more examples must be looked at before drawing further conclusions.

^{iv} It should be noted that the Bugs EcoCodes include five indicator classes, which have slightly different implications from the general habitat classes (see Chapter 4).

^v Significance testing of coefficient values is not yet implemented in BugStats, and these results should be treated as general approximations until tested.

2. The Edge habitat reconstruction values reflect its spatial position and species composition, i.e. in between the other two habitats, but more similar to the Farmland, which is supported by the correlation coefficient values (Table 6.2). The reconstruction of the winter climate also reflects this to a limited extent.
3. The reconstructed TMax span is narrower than the present day (1971-2000) span in central-southern Finland, whereas the reconstructed TMin span is wider than the present day span. The reconstructed temperatures are compatible with the recorded values, within the level of accuracy expected from MCR, but this clearly displays the lower resolution of winter temperature reconstructions.

Table 6.3. MCR thermal reconstruction for Koivula *et al.* (2004) reconstructed grouped trap data. All groups produced 100 % overlap regions. Present day climate for southern Finland given for comparison^{vi}. See Chapter 5 for explanations of the reconstruction method and variables.

Sample	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi	NSPEC
Forest	15	18	-15	4	12	30	20
Edge	16	18	-14	1	16	30	26
Farmland	16	18	-14	-1	19	30	35
Present day climate (1971-2000), July and February respectively							
	13.7	20.9	-7.7	-2.2	Helsinki (60°10'N, 24°56'E)		
	10.4	21.3	-12.9	-5.0	Jyväskylä (62°24'N, 25°40'E)		

6.1.5 Further discussion

The selection of standardization and transformation options is evidently extremely important, and it is recommended that *all* output options are tested, and that the implications of each are understood thoroughly before interpreting the diagrams. A critical difference between the Bugs EcoCode classifications and the habitat groups used by Koivula *et al.* is that the former allow a species to be assigned to more than one class. Broadly eurytopic species (Generalists) therefore, may represent several environments, whereas stenotopic species will represent only one. This is why the sum of represented environments (SumRep) is always higher than the associated sample abundance or number of species (NSpec). Only one species in the dataset (*Loricera pilicornis* (F.)) was indicative of both *Woodland and trees* and *Disturbed/arable*, a designation which most likely represents the commonality of shaded habitats within forests and tall crops (Lem Dahl, *pers. comm.*). Such microhabitat factors are difficult to cater for in general habitat classification systems, and the example serves to demonstrate the need for detailed entomological knowledge when interpreting results based on classification. A comparison of the respective groupings (summarized in Table 6.4, see digital appendix for full species comparisons) shows a reasonable agreement, with only three stenotopic species (with only one Bugs EcoCode classification) having possible conflicts between the systems.

BugStats includes indicator classes for *Deciduous* and *Coniferous* woodland – neither of which was indicated by the fauna. In other words, none of the Carabidae collected in this experiment are considered, as far as the BugStats system is concerned, as woodland indicator species at the European level. At the moment there are nine species of carabid classed as *Deciduous* indicators, and only two classed as *Coniferous*. It could be that the Bugs EcoCodes require revision in this area, although sources such as Lindroth (1945, 1985, 1986) should include a good understanding of North European coniferous forests, even if Koch's (1989-92) data are more Central European and deciduous. Alternatively, the explanation could be more ecological, in that the Carabidae are more tied to the

^{vi} TMax/TMin limit equivalent values. The transects (at 61°30'-61°80'N, 24°55'-25°50'E) most likely experienced a climate between the values from these stations. Data from Finnish Meteorological Institute (FMI) http://www.fmi.fi/weather/climate_6.html

environment of the woodland than the actual wood and trees themselves. That is to say they thrive in the shade and humidity provided by the forest cover, and in some cases prey on other species that are more specifically tied to the actual trees. An ideal study of the forest-arable interface should include as many Coleoptera taxa as possible to reduce the risk of generic level habitat preference traits biasing the results.

Table 6.4. Comparison of number of species per group/classification.
Note that BugStats allows species to fall into more than one class.

Number of Species per habitat group/class			
Koivula <i>et al.</i>		BugStats	
Forest (F)	13	Wood and trees	23
General (G)	12	Meadowland	11
Open (O)	34	Wetlands/marshes	18
Sum	59	Disturbed/arable	13
		Sandy/dry disturbed/arable	16
		Heathland & moorland	11
		Other	3
		Sum	95

6.1.6 Conclusions and implications for BugStats

One might expect the BugStats system to dilute the habitat signals of eurytopic species, as these species count values are spread among several classes. Such species give ‘false’ positive signals of the other habitats that they *could* survive in, in addition to the one that they currently occupy. This is of particular relevance when considering the differences between the interpretation of modern and fossil datasets. When dealing with fossil assemblages this reflects the reality of environmental reconstruction, in that we cannot know *exactly* which of the habitats are being reflected, and we can only use professional judgement to derive the most probable reconstruction. With modern datasets it is often possible to go out and survey the contemporary sampled environment, if it has not already been done in connection with the sampling. By complementing the fossil insect analyses with investigations based on other proxy sources (e.g. pollen, plant macro fossils etc.), one can often improve on the reconstruction by refining the probability of certain environments having existed.

It is a common misconception that post-modernism and empirical science are incompatible, the argument being something as follows: ‘As the past is not directly measurable, and its interpretation is a product of the subjectivity of the researcher, then a number of possible interpretations are equally valid. Hence we can not possibly know *anything* about the past and *all* interpretations are equally valid’. Readers will notice the considerable jump in logic from sentence one to two, which, it should be noted, is more often made by archaeologists and not the philosophers and historians of science from which it is derived. The ‘truth’ of the matter is that several possible interpretations are valid for any reconstruction, and a good publication will present this fact, either by describing a number of possibilities or presenting a measure of uncertainty or probability around the chosen interpretation. Suffice it to say that this is a discussion that has been ongoing within geography and archaeology for many decades (see e.g. James, 1972; Trigger, 1989), and in its essence for many centuries (see e.g. Simmons, 1993). Archaeology, ironically, appears to have a limited ability to allow for a plurality of ideas based on empirical evidence, but this may of course just be a phase that it is going through (Yoffee & Sherratt, 1993)^{vii}.

^{vii} It is perhaps a more serious matter when these misconceptions on our ability to interpret the past influence government policy on research and museum funding, as may be in danger of happening in Sweden (see e.g. Sundborg, 2006)

The slight difference in reconstructed temperatures from the Forest and Farmland habitats reinforces the importance of the effects of large scale vegetation on microclimates. This implies that habitat reconstructions should be studied along with MCR results, as different habitats may differentially bias regional reconstructions. However, the temporal and spatial resolution of palaeoenvironmental samples may reduce such effects, due to the fact that samples will generally have collected species from a wider variety of habitats and climates than samples from modern habitat specific studies. In addition, the evidence of a single study is insufficient evidence to draw further conclusions, and more modern dataset will have to be analysed from a wider range of habitats.

The reconstruction created by BugStats gives a reasonable reconstruction of the habitats described by Koivula *et al*, and possibly gives an indication of the surrounding species catchment area. This case study helps to reinforce the viability of BugStats for palaeoenvironmental reconstruction, by illustrating its ability to reconstruct reasonably accurately a known modern environment. As with any semi-quantitative method, the errors involved in the reconstruction are difficult, if not impossible to calculate. Some Quaternary scientists would perhaps claim that this reduces the power of the method when compared to other quantitative methods. I would disagree, and counter claim that many quantitative environmental reconstruction methods are in fact just as semi-quantitative as BugStats, and that the use of advanced statistical methods to provide standard errors does not elevate them automatically to a higher level of realism. The use of resampling methods on the other hand, which can be applied to semi-quantitative methods, to calculate resampled standard errors is a valuable technique for assessing the relative reliability of reconstructions with respect to the faunas that underpin them.

6.2 Fossil Case Study: 140 000 year Peat Sequence, La Grande Pile, France

Primary reference: Ponel, P. (1995).

6.2.1 Aims

Ponel (1995) studied the beetle fauna from approximately 13 m of multiple cores from a 19 m deep, 140 ka year long peat sequence from the Grande Pile peat bog in eastern France. The ombrotrophic bog is 25 ha in area, and lies at 325 m above sea level. In an impressive piece of work, Ponel identified 394 taxa, including 19 species no longer present in France, from 41 samples, and undertook an environmental and climatic reconstruction from this data. Ponel grouped species by habitat in much the same way that Bugs EcoCodes do, although the systems were developed independently^{viii}. This, and the presentation of his results as environmental indication diagrams displaying number of taxa and species (reproduced here with the permission of the author), makes the site an ideal case study for comparison with BugStats and BugsMCR outputs. In particular, the importance of standardization is apparent in some of the differences between Ponel's figures and those produced by BugStats.

For further descriptions of the site, samples, and other analyses from La Grande Pile readers should refer to the original paper. Similarly, there is no need to repeat detailed descriptions of the faunal changes here, apart from where they aid the discussion on the comparison of classification comparisons.

6.2.2 Methods

It was necessary to add a number of more southern taxa to BugsCEP to enable the entry of the Grande Pile list, and these new taxa have no climate data in the database, which could explain some of the differences between Ponel's MCR reconstruction and that produced by BugsMCR. The reasonable

^{viii} The classifications used in BugsCEP are influenced by his work, among others.

numbers of taxa and individuals present in many of the samples allowed for a wider variety of BugStats settings to be tested. Plots were produced both with limiting the calculations to only those individuals identified to species level as well as for all taxa. This allowed a greater degree of data interrogation, the limited plots theoretically providing more trustworthy reconstructions in that the more broadly categorized generic identifications (sp., spp., indet. in BugsCEP) are omitted. The implications of the differences between these plots are discussed below, along with both a general environmental interpretation focussing on the similarities and differences between Ponel's account and that produced by BugStats.

Ponel classified the Coleoptera into "...several categories according to their ecological requirements..." and, although BugsCEP does not have direct equivalents for all of his categories, the respective classes are shown in Table 6.5 for comparison. In addition, Ponel listed the number of taxa dependent on a number of specific plant taxa, which will not be compared here. Such analyses require only standard BugsCEP information retrieval (browsing and site reporting), and not the use of EcoCodes, which do not hold that level of detail.

Table 6.5. Comparison of Ponel's ecological requirement categories and Bugs EcoCode equivalents. Bugs EcoCodes that are not directly equivalent to Ponel classes are shown in *italics*.

Ponel classes (Ponel, 1995, p7)	Nearest Bugs EcoCode equivalent
Aquatic	Aquatics
- Standing-water	Indicators: Standing water
- Running-water	Indicators: Running water
Terrestrial	All except the above
Riparian species (that live on the shores of standing-water or on river banks)	<i>No direct equivalent, but possibly a combination of Wetlands/marshes and Open wet habitats</i>
Coprophagous (directly dependent on mammal faeces)	Indicators: Dung, and possibly Pasture/Dung and Dung/foul habitats.
Coprophilous (indirectly dependent on mammal faeces)	Dung/foul habitats, and possibly Pasture/Dung
Necrophagous species (that live on dead animals)	Carrion
Tree-dependent species, and deciduous/conifer dependant.	Wood and trees, Indicators: Deciduous and Indicators: Coniferous, respectively
Plant detritus feeders	<i>No direct equivalent, but possibly a combination of Dung/foul habitats and Mould beetles</i>

It is important to remember that while Ponel presents numbers of taxa and individuals, BugStats presents numbers of environmental representations, that is to say counts of the number of taxa that represent an environment. These values may be abundance weighted, or not, and optionally standardized, producing four different plots from the same data (excluding the log transformation option). It is also possible to limit the BugStats calculations to only taxa identified to species level, thus potentially increasing the reliability of the environmental indications displayed. All eight of these plot possibilities are presented below, but only selected components are described with reference to Ponel's work.

6.2.3 Results and general comparison

The Grande Pile fauna produced some kind of signal in all Bugs EcoCode categories, with the exception of *Stored grain pests* and *Ectoparasites*. The latter is hardly surprising due to the rarity of these finds in natural deposits, their concentrations, at least in present day Europe, being too few without natural herds or human concentration of animals. There is, however, very little known about

the extent of herbivore herds in Europe in the past^{ix}, and investigations of potential watering holes would probably be necessary in order to even tentatively identify them from the insect faunas. Finding these deposits is, unfortunately, potentially even more difficult. Pests of stored products are almost equally rare in natural deposits, with perhaps the exception of direct sampling of packrat middens (Elias, 1994) or the burrows and nests of other animals that collect seeds.

The presence of synanthropic species is interesting, and may be a reflection of a North European bias in the database's sources. It may also indicate that what we consider as synanthropic species today have previously been a consistent part of the natural background fauna. Although filtering out generic level identifications almost entirely removes these (Figure 6.4), it would be interesting to see what proportion of these species could be captured by pitfall trapping on the bog today.

Besides the groups discussed below, a number categories produce almost continuous background signals, especially in the 'All taxa' diagrams (Figure 6.4). These include: *Meadowland*, *Heathland/moorland*; and to a lesser extent: *Open wet habitats*, *Disturbed/arable*, *Sandy/dry disturbed/arable*, *Halotolerant*. At least two of these, *Heathland/moorland* and *Open wet habitats* are explainable in terms of the local bog environment, and their persistence after the removal of generic level identifications reinforces this. *Meadowland* species may reflect a number of possible environments including naturally grazed grasslands, which would be supported by the *Pasture/dung* component, or other open landscapes with flowers and grasses. The other categories may, to an extent, be artefacts of generic level identifications representing a larger spectrum of habitat possibilities.

The effects of filtering the calculations to species level only vary between habitat group and sample. Some of the effects on groups will be the inevitable consequences of the removal of taxa from other groups, thus raising the percentage representation of the others. The sum of representations (SumRep) is calculated on the filtered counts, however, so this effect is internal to the particular diagram set (for a discussion of identification and taphonomic influences on environments represented, which will not be discussed in detail here, see Chapter 4). A number of general patterns are immediately obvious when comparing the 'All taxa' (Figure 6.4) and 'Species level identifications only' (Figure 6.5) diagrams:

1. Peaks and troughs are more pronounced in the species level only %SumRep than in the equivalent for all taxa, despite the reverse being true for the abundance and taxa sums (Figure 6.6). This may be an indication of a relationship between abundance and preservation, in that samples with higher abundances may also have better preservation, and *vice versa*.
2. A number of categories increase their % representation dramatically, with an increase by up to 65 % in some cases: *Aquatics*, *Indicators: Standing water*.
3. Some categories decrease their % representation significantly, becoming intermittent minor signals in the profile: *Open wet habitats*, *Meadowland*, *Pasture/dung*.
4. Some categories almost completely disappear: *Carrion*, *General Synanthropic*, *Halotolerant*.
5. A few categories remain essentially the same, as small, intermittent signals: *Indicators: Dung*, *Dry dead wood*.

By standardizing the data it is possible to obtain a picture of environmental change that is less dependent on the number of taxa or individuals in each sample. This is not without its interpretive implications, and readers should refer to the explanation of the standardization routine in Chapter 4 for more details.

^{ix} See the discussion of Frans Vera's work with respect to the insect evidence in Buckland [*et al.*] 2005.

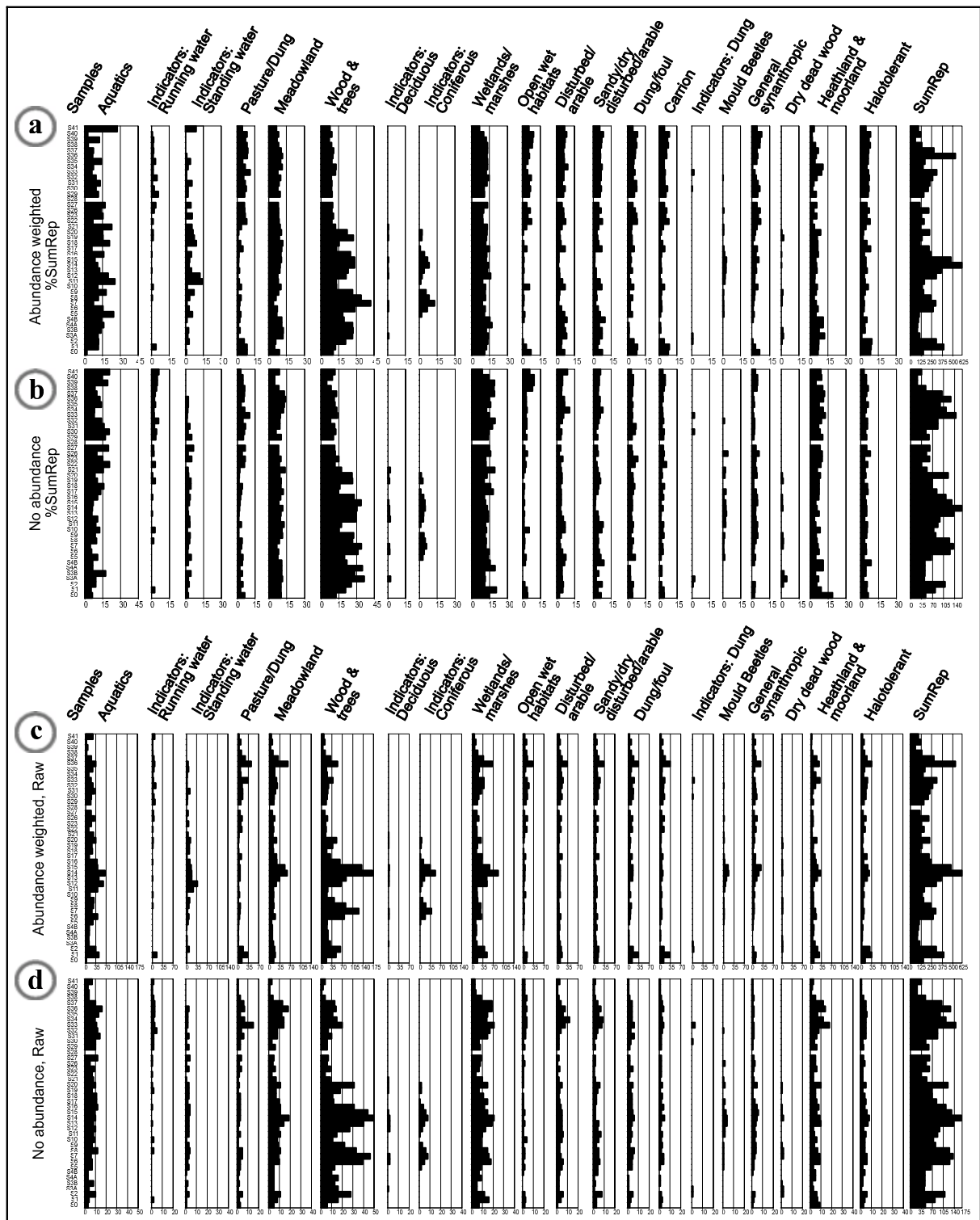


Figure 6.4. All taxa EcoFigs for La Grande Pile. Diagrams (a) and (b) show abundance weighted, and taxa only, standardized values respectively. Diagrams (c) and (d) show abundance weighted, and taxa only, raw values respectively. Number of taxa and abundance totals are shown in Figure 6.6.



Figure 6.5. Species identifications only EcoFig for La Grande Pile. Diagrams (a) and (b) show abundance weighted, and taxa only, standardized values respectively. Diagrams (c) and (d) show abundance weighted, and taxa only, raw values respectively. Number of taxa and abundance totals are shown in Figure 6.6.

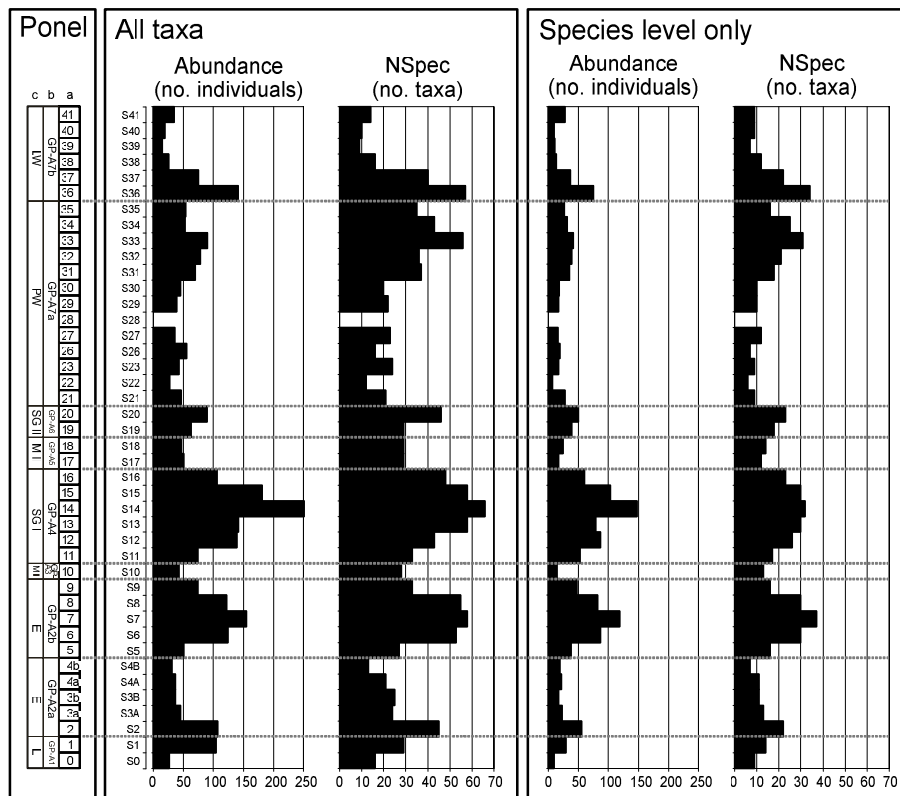


Figure 6.6. La Grande Pile, comparison of number of taxa and individuals, showing all taxa and species level only identifications for comparison. Panel's (a) samples, (b) faunal units, and (c) the pollen chronozones of Beaulieu & Reille (1992) are shown. Note the different scales on abundance and NSpec graphs.

6.2.4 Discussion and detailed comparison of specific habitat groups

Ponel presents figures illustrating the variations in numbers of taxa and individuals that represent three particular habitat groups: tree-dependent species, aquatic species, and coprophagous species. A comparison of the equivalent classes (Table 6.5) in BugsCEP is presented here, in addition to a discussion of the problems with using raw abundance data for inter-sample comparisons, and the potential effect of standardization on interpretations. The BugStats plots which are most structurally similar to those of Ponel will be used as the basis for discussion, with other plots being presented where there are interesting differences, or to illustrate a point.

Note that the indicator classes in BugsCEP consist entirely of species level taxa, with the single exception of *Hydaticus* sp. This water beetle genus in particular is described as being totally dependent on standing water bodies, but it may be that other genera can be added to the indicator classes in later versions after discussions with the relevant experts.

It may be prudent to remind the reader of the long time scales involved with the interpretation of this data. With the insect samples covering approximately 110 000 years (see Ponel, 1995, for dates), the average time span covered by each sample is c. 2 700 years. Much can occur in such a space of time, including such difficult to entomologically define episodes as the Little Ice Age (Wagner, 1997), or the Younger Dryas, let alone the 8 200 cal. yrs BP event (Edwards *et al.*, 2006; see also Bennett, 2002, for a discussion of dating and correlation difficulties). As a result of this the faunas are likely to be mixed as the environment around the bog changes, and samples that overlap dramatically different phases, be they climatic or other environmental in nature, will provide a signal which indicates both of these environments. In the MCR results this will most likely result in a non-100 % overlap situation, which could theoretically be resolved by extracting a warm and cold faunal component from the data (see Chapter 5). Resolving the environmental signal is more difficult, as there are a number of classes involved, and doing so would necessitate even more circular reasoning than the MCR faunal

component concept. This said, the data still present a compounded environmental signal for each set of environments represented by the samples, which gives us valuable insights into the past 140 000 years of landscape change in the area around La Grande Pile. This in itself is one of the most complete records of long term environmental change that exists for Europe.

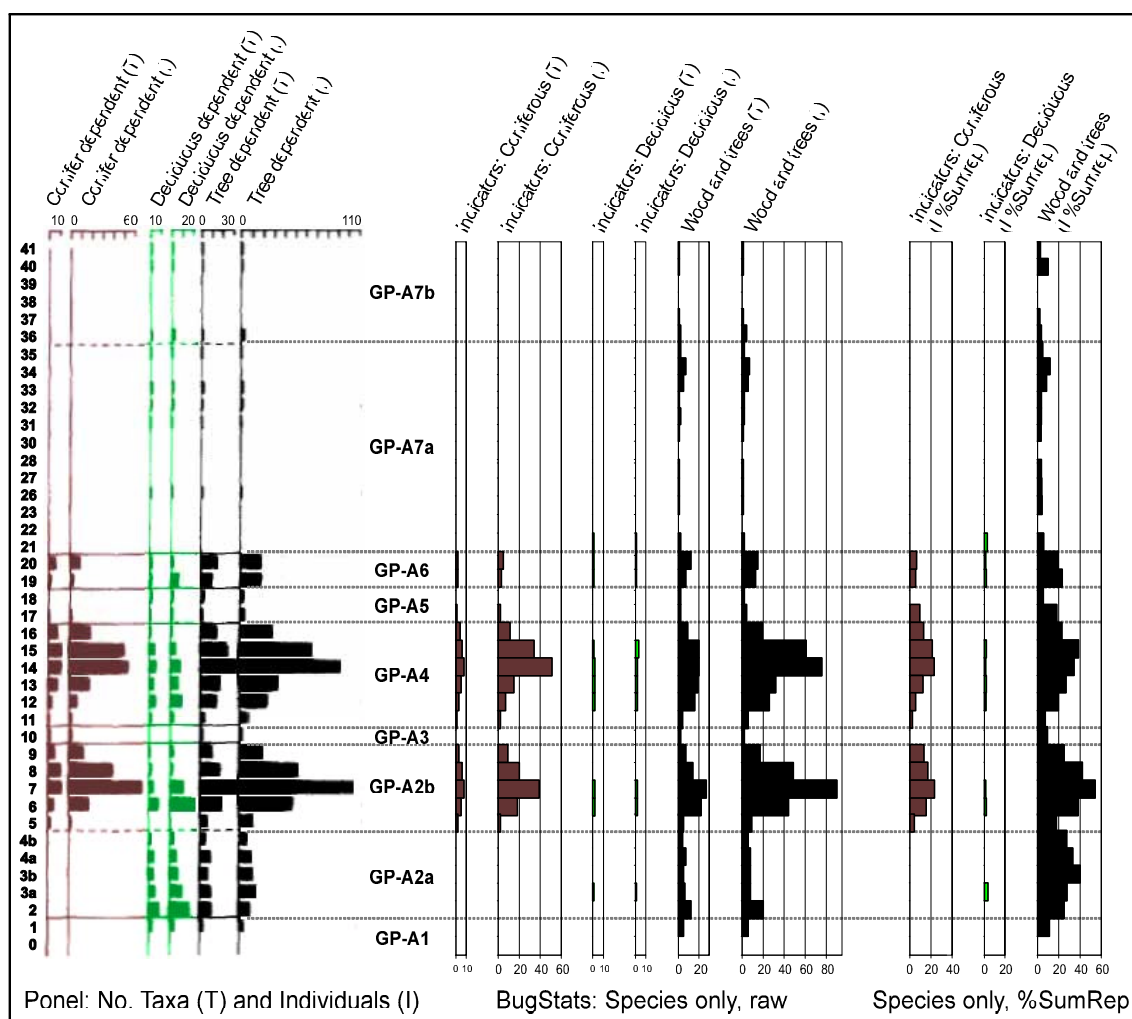


Figure 6.7. Comparison of woodland habitat numbers for Ponel's classes: Conifer dependant, Deciduous dependant, Tree-dependent; and the equivalent raw, species level identification only, representation counts in BugsCEP: *Indicators: Coniferous*, *Indicators: Deciduous*, *Wood and trees* respectively. T = No. of Taxa, I = No. of Individuals. Sample 29 is absent from the original figure and therefore also the BugStats charts.

The Tree-dependent and *Woodland and Trees* plots are almost identical between systems (Figure 6.7), including the standardized (%SumRep) plot to a certain extent. This shows a large degree of agreement in the classification of species by habitat. However, when it comes to comparing the indicator species with Ponel's deciduous and coniferous dependent groups there are a number of differences. BugStats does not show more than a single specific indication of deciduous woodland below sample 6, whereas Ponel shows deciduous dependent species in all but sample 0, with a peak in sample 2 almost equivalent to that in sample 6. There are in fact very few deciduous indicators in the sequence according to the BugsCEP classification, and there is obviously a significant difference in the classification systems in respect to this. This may be an aspect of the north European bias of BugsCEP, and the need for more data and a review of the classification system. It may also indicate that many of the taxa regarded by Ponel as being deciduous dependent are less so in northern Europe. The conifer indicators/dependent categories, although with slightly lower values in BugStats, show considerable similarity. There appear to be fewer *Wood and trees* species in BugsCEP than in Ponel's

tree dependent group, which is surprising, as the former class includes species less specifically tied to woodland, and more to the shaded environments provided by trees as well as those specifically dependent on wood or leaves. The inclusion of generic level identifications (Figure 6.4) gives this category a higher background signal, but does not change the structure of the peaks and troughs.

The %SumRep standardization of the abundance weighted species only data has some interesting implications for the interpretation of the woodland/tree categories (Figure 6.7). Whilst reducing the two most prominent peaks, it produces a peak between samples 1 and 4B comparable with that between samples 12 and 16. The implication of this is a much earlier woodland development in the sequence, at the start of Ponei's faunal unit GP-A2a, rather than later in GP-2b.

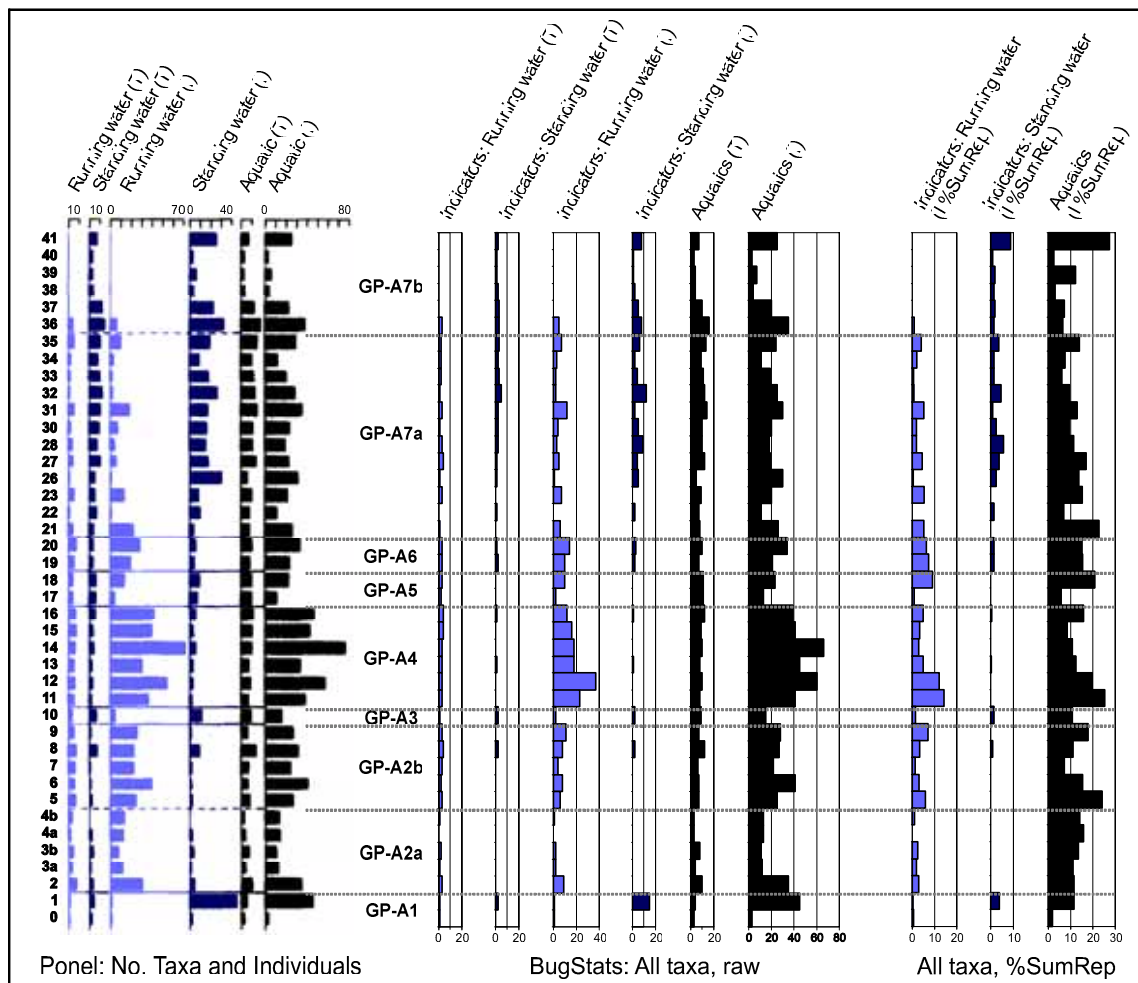


Figure 6.8. Comparison of aquatic habitat numbers for Ponei's classes: Aquatics, Standing-water, Running-water; and the equivalent for all taxa in BugsCEP: *Aquatics*, *Indicators: Standing water*, *Indicators: Running water* respectively.

As with the woodland diagrams above, the general Aquatic groups match very well, both in number of taxa and individuals (Figure 6.8). This may reflect the fact that most water beetles are very easy to define as such, and their ecology is well known (e.g. Foster, 2000; Nilsson & Holmen, 1995). Although the trends are generally the same, the indicator type classes differ a little. This may primarily be due to a reluctance in BugsCEP to define species as either *Standing* or *Running water* dependent unless it is universally so for the BugsCEP dataset. In addition, generic level identifications have not been assigned to indicator groups, and it can be seen from the data that Ponei uses the former in his reconstruction. As discussed earlier, the use higher level taxon as indicators may be valid for a limited region, but as Bugs EcoCodes are designed to be more regionally independent, then indicator classifications at the generic level are risky.

Standardization of the data makes some of the clusters visible in the raw data difficult to resolve. In particular, the lowest peak in aquatic individuals (samples 1-2) merges completely into the samples above it. As the total number of individuals in these samples is high (104 and 107 resp.), an explanation in terms of large percentage swings due to low numbers can be discounted, and one must look to the other habitats with which it is standardized for clarification. From Figure 6.4a (or indeed Figure 6.4c), we can see that although the number of aquatic individuals is high, there is an equally high signal in *Wood and trees* and *Wetlands/marshlands*, and almost as high in *Halotolerant*, *Heathland & moorland* and *Pasture/Dung*. This represents quite a varied landscape of woodland, bog, grassland and moorland with lakes or streams. This illustrates, of course, that whilst changes in abundances for one group of insects on its own is interesting, it must be put in a landscape perspective for a fuller reconstruction. There is a similar peak reduction effect at samples 35-37, although part of the peak, at 35, remains. This appears to be reflected in a slight decrease in the *Pasture/Dung* signal, possibly indicating a wetter period with generally fewer grasslands and grazing animals, as shown in Figure 6.9.

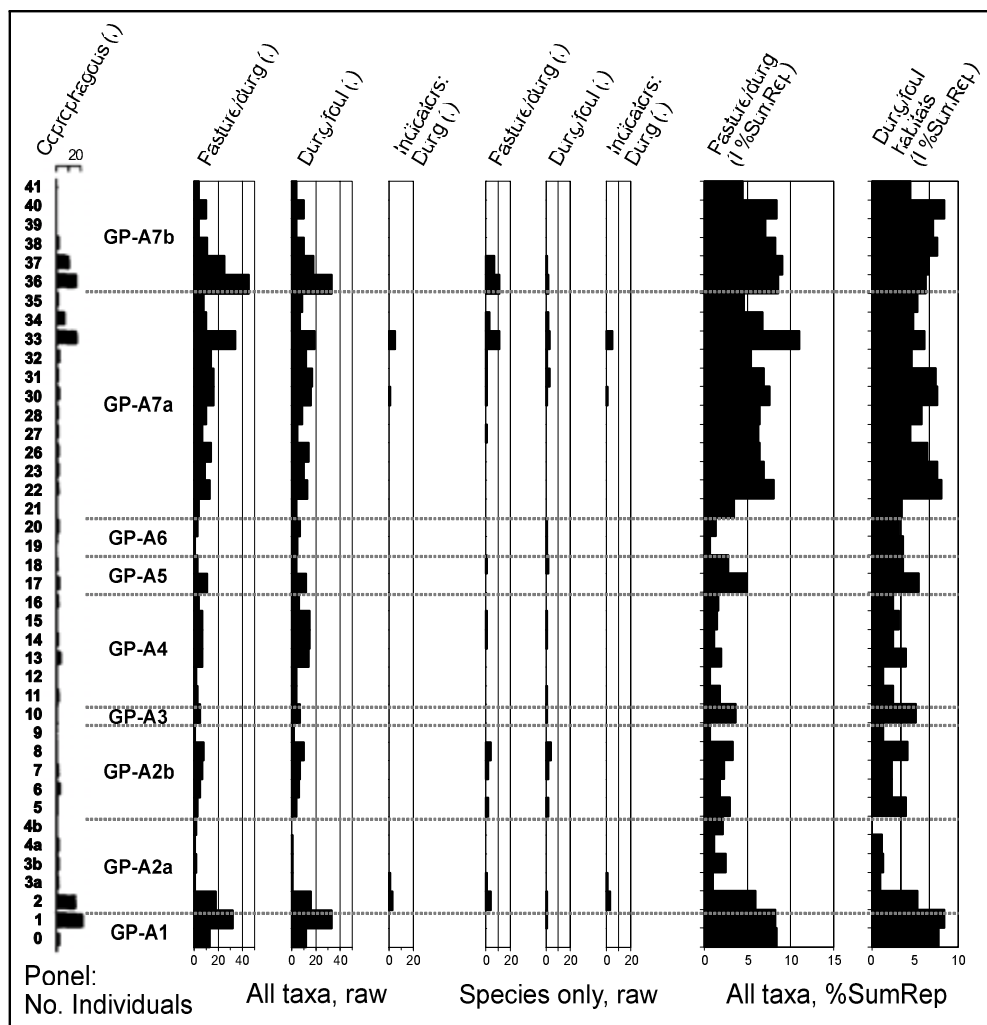


Figure 6.9. Comparison of dung habitat numbers for Pönel's coprophagous class and the equivalents in BugsCEP: *Indicators: Dung*, *Dung/foul habitats* and *Pasture/dung*. Note the different scales.

BugsCEP includes three EcoCode categories that may give indication of the presence of dung: *Indicators: Dung*, *Dung/foul habitats* and *Pasture/dung* (Figure 6.9). These are designed to include a large part of the full range of coprophagous (feeding on dung) and coprophilous (found in dung) beetles. The specificity of habitat requirements of dung beetles varies, and so a dung beetle does not always definitely indicate the presence of dung. Some species are as likely to be found living in wet

mud, although many must breed in dung (Skidmore, 1991). Part of the need for these different classes is that archaeological sites can have had a number of ‘dung like’ deposits, such as middens, that attracted dung beetles without there necessarily being domestic animals present. The indicator class is logically the most restrained, and is the most definite indicator of dung, and thus animals in the surroundings, modern comparative work suggesting that even small numbers of some of these species are indicative of the presence of animals (Lemdahl, *pers. comm.*). Ponel’s number of coprophagous individuals diagram most closely resembles the species only, raw, *Pasture/dung* output from BugStats, with the exception of the lowest two-three samples. Closer examination of the fauna show that the latter is entirely due to the exclusion of *Aphodius* spp. from the BugStats diagram. It seems that the two classification systems do not completely mesh in this case, where although the genus *Aphodius* is largely a dung indicator, it does include several species (e.g. members of the subgenus *Aegolius*) which prefer rotting plant debris, and the uncertainty in the identification excludes it from the most comparable diagram. The ‘All taxa’ diagrams include counts for *Aphodius* spp., but are far broader than Ponel’s group, and thus indicate a greater variety of habitats.

The above may serve to illustrate the importance of examining the fauna in detail, even with the advantage of semi-automated habitat reconstruction software. The standardized diagrams (Figure 6.9), their scales expanded here for clarity, suggest a clear polarity in the sequence, with animals present in larger numbers at the bottom (0-2) and top (22-40/41), similar to that described by Ponel, but more extended. This is almost in direct antiphase with the woodland signals (Figure 6.7), but is closer to the open habitat signals (Figure 6.4). As noted by Ponel this corresponds closely with the colder phases of the sequence (Figure 6.10).

Although the precise details of the climate reconstruction system used by Ponel are not known, one can assume that the majority of the reference dataset is the same as that used in BugsMCR, which is part of the reason why the figures are so similar. There are a number of samples where the reconstruction of Ponel produces significantly more constrained temperature limits, especially for TMin: samples 19, 9, 4a, 3a and 1 are the most pronounced. In the bottom three of these the difference can be explained by less stenothermic envelopes defined in the BugsMCR dataset for low number of species (2, 2 and 1 resp.). These relatively warm tolerant species, *Poecilus lepidus* (Lesk.), *Agabus sturmii* (Gyll.), *Chaetarthria seminulum* (Hbst.) and *Coelostoma orbiculare* (F.) will have to be examined and their envelopes possibly revised. A number of other samples display narrower temperature ranges in the BugsMCR reconstruction, in particular, samples 37, 33 and 30. None of these samples have a 100 % overlap area, and it may be that Ponel has chosen to omit species in order to simulate one, rather than calculate temperature values from the nearest maximum area, as BugsMCR does when instructed.

The issue of overlap percent and sample representation is interesting, in that samples without 100 % overlap areas by definition must represent more than one, or a gradient along, temperature regimes. It may also be possible to extrapolate this further by suggesting that they may also represent more than environment and thus different sets of habitats. Although the function to extract warm and cold components from the fauna is not yet implemented in BugsMCR (see Chapter 5), the appropriate data and structure are in place, and it would be an interesting experiment in theoretical biogeography to reconstruct the environments represented by these components. Interestingly, sample 34, which has a comparable number of species to many of the non-100 % overlap samples, did produce a 100 % overlap reconstruction. This suggests an unusually stable temperature regime, or alternatively a much shorter time-span captured by the sample. There also appears to be no or very little relationship between reconstructed temperature and number of species^x, which is unusual, as more temperate climates usually support more species than arctic ones (e.g. Rosenzweig, 1995).

^x At most significant is with ln(TMin upper limit) at $R^2=0.2$.

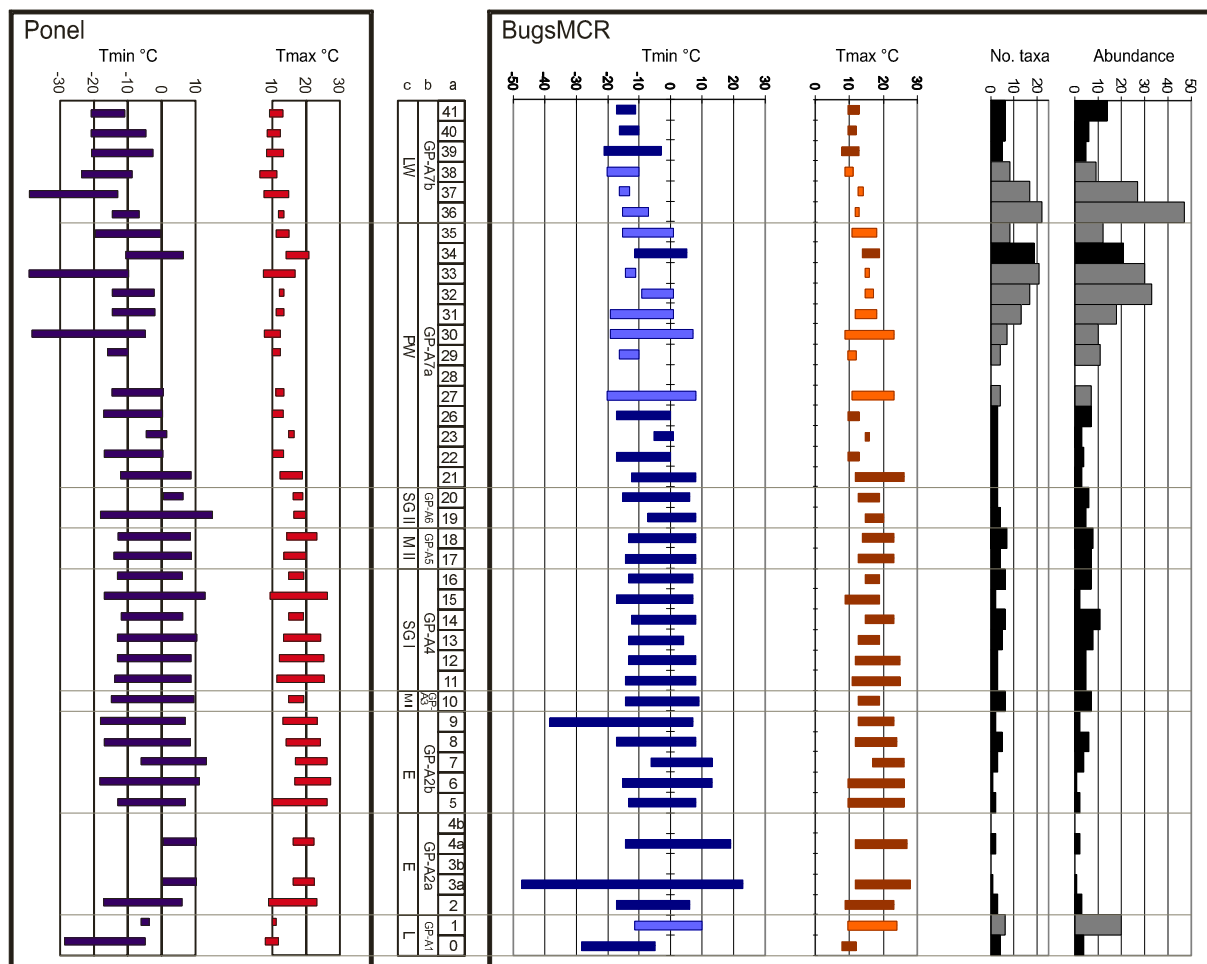


Figure 6.10. A comparison of the BugsMCR temperature reconstruction for La Grande Pile with that provided by Ponel. Numbers of taxa and individuals used in the BugsMCR calculations are provided on the right, and samples where the area of maximum overlap contains <100 % of taxa are indicated by lighter shading.

6.2.5 How are Ponel's faunal and chronological groups affected by the use of standardized results and sample correlations?

Division of stratigraphic sequences into faunal units is a difficult task, and although a number of methods such as cluster analysis and ordination can be employed (Jongman *et al.*, 1995), the fine tuning of the division between units is as much an art as a science. Faunal units can be derived by statistically assessing the similarity between sample faunas, and then applying any of a variety of clustering algorithms to group samples by similarity and stratigraphic position (Kovach, 1995). A semi-quantitative approach, more common in palaeoentomology, is to identify significant changes in faunal signals by examining plots such as those used above, and with reference to, if available, MCR and other proxy data.

The BugStats correlation matrix output, comparing each and every sample fauna from La Grande Pile, is shown in Table 6.6. This could be used as the foundation for cluster analysis proper, but is used here to provide support for the statistical grouping of possible faunal units in the sequence. As can be seen there are a number of patterns in the similarity of neighbouring samples (represented by the values of the diagonal edge of Table 6.6), similar in many respects to those described by Ponel (1995). Coefficient values were used to group more like samples together, using an arbitrarily defined drop in similarity to define borders. Sequences of dissimilar samples were also grouped together, for the sake of simplicity, but the lack of similarity between adjacent samples suggests a high degree of variation in the faunas, and thus the environments represented by them (Figure 6.11). Ponel's brief faunal unit descriptions (Ponel, 1995: p26) are quoted below for comparability. Refer to Figure 6.11 for the labels

used in the comparisons below, and previous figures for details of the habitat signals and temperature values.

Table 6.6. Correlation matrix showing modified Sørensen's coefficient (Southwood, 1978) between La Grande Pile samples. Darker shading represents greater similarity between sample pairs, and coefficient values are on a scale from 0 = no similarity, to 1 = total similarity.

	S41	S40	S39	S38	S37	S36	S35	S34	S33	S32	S31	S30	S29	S27	S26	S23	S22	S21	S20	S19	S18	S17	S16	S15	S14	S13	S12	S11	S10	S9	S8	S7	S6	S5	S4b	S4a	S3b	S3a	S2	S1		
S41																																										
S40	0.41																																									
S39	0.40	0.41																																								
S38	0.23	0.55	0.40																																							
S37	0.31	0.38	0.27	0.38																																						
S36	0.20	0.20	0.13	0.20	0.52																																					
S35	0.31	0.27	0.20	0.30	0.40	0.36																																				
S34	0.05	0.03	0.03	0.13	0.23	0.27	0.22																																			
S33	0.10	0.18	0.11	0.23	0.34	0.36	0.26	0.35																																		
S32	0.23	0.23	0.11	0.29	0.35	0.40	0.39	0.24	0.33																																	
S31	0.10	0.22	0.12	0.25	0.28	0.29	0.52	0.24	0.25	0.42																																
S30	0.23	0.38	0.13	0.34	0.40	0.32	0.48	0.16	0.28	0.42	0.38																															
S29	0.35	0.38	0.15	0.34	0.32	0.28	0.41	0.20	0.29	0.46	0.29	0.55																														
S27	0.31	0.25	0.20	0.30	0.34	0.28	0.47	0.22	0.24	0.35	0.32	0.49	0.43																													
S26	0.44	0.38	0.23	0.28	0.46	0.33	0.31	0.07	0.25	0.35	0.26	0.44	0.36	0.40																												
S23	0.18	0.26	0.21	0.24	0.27	0.21	0.42	0.17	0.24	0.23	0.34	0.39	0.32	0.38	0.31																											
S22	0.29	0.61	0.29	0.42	0.43	0.29	0.35	0.05	0.26	0.25	0.25	0.53	0.42	0.38	0.51	0.38																										
S21	0.15	0.15	0.16	0.14	0.13	0.12	0.20	0.06	0.09	0.16	0.12	0.20	0.19	0.22	0.16	0.39	0.22																									
S20	0.03	0.04	0.04	0.05	0.09	0.11	0.15	0.08	0.07	0.11	0.18	0.09	0.09	0.13	0.13	0.21	0.09	0.34																								
S19	0.02	0.00	0.00	0.02	0.06	0.08	0.10	0.05	0.01	0.06	0.12	0.02	0.04	0.08	0.07	0.19	0.00	0.33	0.53																							
S18	0.07	0.03	0.03	0.08	0.15	0.14	0.20	0.16	0.10	0.14	0.21	0.11	0.14	0.22	0.08	0.27	0.08	0.34	0.34	0.31																						
S17	0.14	0.26	0.15	0.32	0.32	0.21	0.34	0.17	0.20	0.29	0.33	0.27	0.33	0.30	0.26	0.30	0.28	0.25	0.21	0.16	0.35																					
S16	0.04	0.03	0.03	0.08	0.08	0.12	0.19	0.13	0.09	0.15	0.22	0.12	0.14	0.18	0.10	0.26	0.06	0.28	0.49	0.34	0.25	0.19																				
S15	0.05	0.05	0.04	0.05	0.07	0.10	0.12	0.06	0.07	0.11	0.17	0.09	0.12	0.10	0.08	0.18	0.07	0.25	0.43	0.32	0.19	0.16	0.56																			
S14	0.04	0.04	0.03	0.04	0.07	0.08	0.10	0.05	0.06	0.10	0.14	0.09	0.10	0.08	0.07	0.12	0.06	0.20	0.35	0.24	0.15	0.14	0.43	0.56																		
S13	0.05	0.05	0.05	0.07	0.11	0.13	0.12	0.09	0.10	0.12	0.16	0.06	0.10	0.12	0.10	0.17	0.07	0.27	0.50	0.39	0.30	0.23	0.54	0.53	0.48																	
S12	0.02	0.03	0.03	0.04	0.07	0.08	0.09	0.05	0.04	0.06	0.13	0.05	0.06	0.08	0.06	0.12	0.05	0.26	0.48	0.41	0.27	0.17	0.46	0.44	0.44	0.52																
S11	0.02	0.02	0.02	0.08	0.07	0.09	0.09	0.09	0.06	0.08	0.18	0.05	0.07	0.15	0.06	0.17	0.04	0.32	0.47	0.41	0.40	0.18	0.38	0.29	0.26	0.45	0.51															
S10	0.13	0.20	0.14	0.15	0.21	0.17	0.23	0.11	0.27	0.13	0.13	0.21	0.22	0.23	0.25	0.29	0.32	0.16	0.08	0.08	0.16	0.26	0.14	0.09	0.08	0.16	0.07	0.09														
S9	0.02	0.02	0.02	0.02	0.05	0.07	0.14	0.05	0.04	0.08	0.14	0.07	0.09	0.09	0.08	0.21	0.06	0.47	0.52	0.54	0.35	0.19	0.49	0.43	0.35	0.47	0.45	0.43	0.10													
S8	0.04	0.03	0.03	0.03	0.05	0.11	0.11	0.08	0.08	0.12	0.18	0.12	0.11	0.13	0.07	0.22	0.04	0.26	0.31	0.28	0.17	0.16	0.32	0.36	0.34	0.30	0.31	0.26	0.11	0.41												
S7	0.03	0.02	0.02	0.03	0.06	0.08	0.10	0.06	0.06	0.09	0.09	0.08	0.08	0.08	0.07	0.14	0.04	0.21	0.33	0.27	0.14	0.15	0.34	0.37	0.33	0.35	0.24	0.21	0.07	0.35	0.51											
S6	0.03	0.01	0.01	0.04	0.05	0.06	0.08	0.05	0.03	0.05	0.08	0.04	0.05	0.05	0.04	0.13	0.04	0.24	0.38	0.31	0.25	0.16	0.33	0.33	0.32	0.40	0.33	0.31	0.04	0.33	0.28	0.45										
S5	0.02	0.03	0.03	0.03	0.05	0.06	0.10	0.10	0.03	0.03	0.13	0.08	0.09	0.07	0.02	0.17	0.05	0.35	0.37	0.33	0.24	0.16	0.29	0.25	0.23	0.31	0.29	0.43	0.06	0.38	0.32	0.30	0.34									
S4b	0.00	0.00	0.00	0.04	0.02	0.03	0.05	0.02	0.02	0.02	0.03	0.06	0.03	0.00	0.14	0.03	0.23	0.22	0.23	0.13	0.05	0.19	0.14	0.13	0.20	0.15	0.25	0.05	0.25	0.13	0.22	0.31	0.46									
S4a	0.00	0.00	0.00	0.03	0.05	0.04	0.09	0.04	0.03	0.05	0.06	0.10	0.08	0.08	0.04	0.20	0.06	0.31	0.29	0.24	0.21	0.14	0.20	0.16	0.16	0.22	0.20	0.22	0.05	0.27	0.14	0.22	0.30	0.36	0.50							
S3b	0.00	0.00	0.00	0.00	0.04	0.06	0.11	0.04	0.03	0.00	0.07	0.07	0.05	0.05	0.02	0.15	0.06	0.17	0.22	0.20	0.24	0.09	0.10	0.11	0.10	0.18	0.16	0.13	0.08	0.23	0.14	0.15	0.26	0.27	0.41	0.51						
S3a	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.00	0.00	0.00	0.00	0.04	0.02	0.00	0.00	0.16	0.03	0.28	0.24	0.24	0.15	0.04	0.12	0.14	0.13	0.17	0.15	0.02	0.22	0.16	0.21	0.31	0.33	0.42	0.56	0.56						
S2	0.01	0.02	0.02	0.05	0.10	0.09	0.10	0.11	0.14	0.08	0.12	0.07	0.08	0.08	0.06	0.17	0.04	0.22	0.22	0.24	0.22	0.16	0.24	0.24	0.21	0.33	0.23	0.28	0.09	0.25	0.15	0.24	0.31	0.29	0.29	0.28	0.22	0.22				
S1	0.17	0.20	0.07	0.17	0.27	0.26	0.25	0.11	0.28	0.25	0.17	0.27	0.31	0.20	0.42	0.18	0.29	0.08	0.08	0.01	0.08	0.21	0.08	0.06	0.08	0.12	0.04	0.06	0.23	0.04	0.06	0.05	0.06	0.05	0.03	0.07	0.07	0.04	0.20			
S0	0.20	0.58	0.29	0.47	0.34	0.22	0.28	0.10	0.28	0.25	0.29	0.42	0.43	0.29	0.37	0.32	0.53	0.14	0.07	0.02	0.05	0.31	0.06	0.06	0.04	0.08	0.02	0.04	0.18	0.02	0.04	0.06	0.04	0.03	0.04	0.03	0.03	0.00	0.09	0.25		

GP-A1:

"...characterized by the occurrence of cold-adapted Coleoptera, the scarcity of tree dependent Coleoptera and the high number of standing-water Coleoptera."

There is general agreement between the woodland, aquatic and dung graphs, although one could possibly extend the boundary to cover sample 2 on the basis of the *Pasture/dung* evidence (B1). The *Wood and trees* evidence, on the other hand supports the original boundary. The standing-water signal of Ponel is not seen in BugStats. The MCR results could support the movement of the boundary, although there is much scope for variation in the temperature of samples 1, 2, and 3. Sample 0 remains significantly colder and could form its own climatically defined unit.

GP-A2a:

"...characterized by the complete disappearance of cold-adapted Coleoptera, the abundance of tree-dependent and running-water Coleoptera. This unit may be divided in two subunits GP-A2a (rich in deciduous tree-dependent Coleoptera but totally devoid of conifer-dependent Coleoptera) and GP-A2b (many conifer-dependent taxa, mixed with deciduous tree-dependent Coleoptera)."

The warmer climate implied by Ponel is partly supported by BugsMCR, although the ranges are large, with a rise in the lower limit of TMax and a raising of the upper limit of TMin. The reported peak in woodland is apparent, but there is too little of a *Indicators: running water* signal in the Bugs EcoCodes to corroborate this group. The division in GP-A2a and GP-A2b is supported, although one sample higher up, with a slight indication of more dung in GP-A2b. Sample 5, on the basis of the *Wood and trees* and *Aquatic* signals could potentially form its own minor unit.

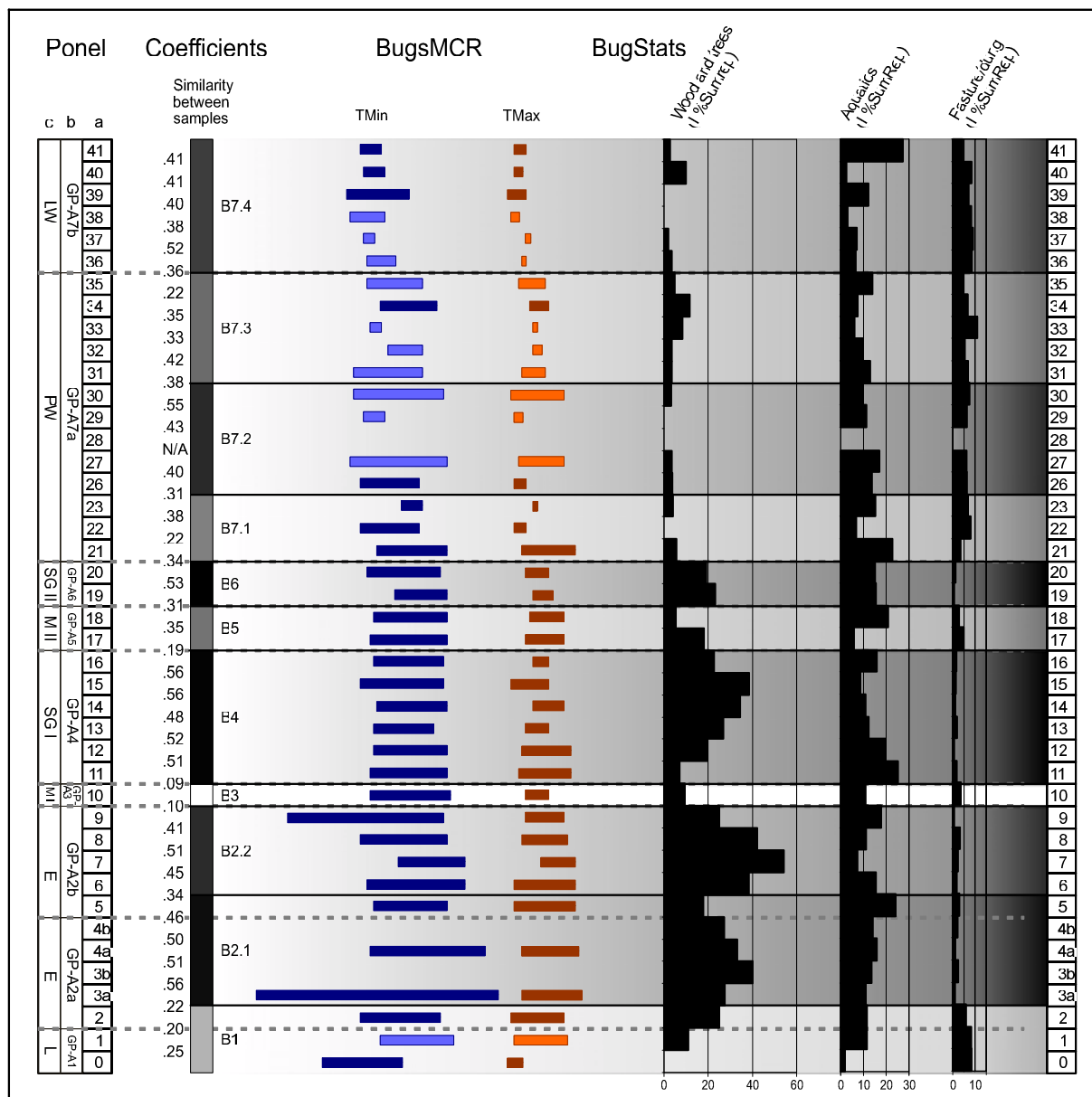


Figure 6.11. Comparison of Ponel's faunal units with those derived from correlation coefficients for neighbouring samples, and possible implications of BugStats standardized outputs on the original faunal units. Coefficient based sample groups (B1-B7.4) are shaded by the average of the coefficient values for samples in the group. 0 = no similarity, 1 = total similarity.

GP-A3:

"...a small unit showing a significant decrease in tree-dependent Coleoptera and the dominance of standing-water Coleoptera over running-water Coleoptera."

This is apparent in the drop and narrowing of TMax, a reduction in *Aquatic* habitats, and a slight increase in *Pasture/dung*. The *Wood and trees* signal is ambiguous in that the graph depression continues into the sample above it. In addition, an examination of the other habitats available (Figure 6.4 and Figure 6.2) suggests a general spread of more *Open wet habitats*, *Disturbed/arable* and *Heathland & moorland* type environments, during a slightly colder period, as Ponel also notes.

GP-A4:

"...this unit is very similar to GP-A2b, but with sporadic occurrence of isolated specimens of the relatively cold-adapted species *Potamonectes assimilis*."

BugStats reveals a lower woodland peak, closer in form and magnitude to GP-A2a than GP-A2b, but with a *Dung/foul habitats* more similar to GP-A2b. There is an interesting long term trend in the reduction of *Aquatics*, primarily generated by running water species (Figure 6.8). The correlation matrix (Table 6.6) shows a slightly higher statistical similarity with GP-A2b than GP-A2a.

GP-A5:

“...fairly similar to GP-A3, with a pronounced decrease of tree-dependent Coleoptera, a slight rise of standing-water beetles and a rare occurrence of cold-adapted taxa.”

A relative doubling of the *Pasture/dung* signal reinforces the definition of this unit, as does the MCR, although this shows a slight rise in possible temperatures despite the presence of cold-adapted species. BugsCEP does not produce any standing water signal for the unit. The standardized *Aquatic* and *Wood and tree* signals are ambiguous, mirroring each other in samples 17 and 18, with 17 having a relatively high *Wood and trees* signal, and 18 having an equally high *Aquatic* signal. The fauna of sample 17 appears to be statistically most similar to samples higher up in the sequence (18, 29, 31, 35, 37, 38) along with the basal sample. Sample 18 on the other hand, is more similar to the two samples directly above (19, 20) and a few samples below (9, 11, 13) in GP-A2b and GP-A4. It is most similar to sample 11, with which it shares very similar MCR results.

GP-A6:

“This unit has similar beetle assemblages to that recorded in units GP-A4 and GP-A2b. Tree-dependent Coleoptera reappear but are less abundant in GP-A6 than in GP-A4 and GP-A2b. There is a predominance of running water Coleoptera. Cold-adapted Coleoptera are rare.”

This unit is clearly visible in all three habitat groups discussed here (Figure 6.11), with woodland signals being elevated well above the adjacent samples. *Pasture/dung* and *Aquatic* signals are lower than the immediately adjacent samples, but the latter is still relatively high at c. 15 % SumRep. The *Dung/foul* signal (Figure 6.9) does not differentiate this sample from its neighbours, suggesting that whilst the grassland type landscape may have diminished, there were still muddy or relatively dung rich habitats nearby. The correlation matrix certainly illustrates that the samples are most similar, as Ponel states, to GP-A4 and to a lesser extent GP-A2b, although sample 9 is most similar to both 19 and 20. It is interesting to observe that sample 10, the probable open, cold phase unit GP-A3, bears almost no similarity at all to GP-A6. The *Aquatics* are dominated by running water species, but BugStats does show the highest proportion of standing water species since samples 10, although it is not much of a signal. The running water signal itself does not differentiate the unit from its immediate neighbours.

GP-A7:

“This large unit is made up of 18 samples. The beetle assemblage shows a great change compared with the lower samples. The tree-dependent taxa disappear almost totally, cold adapted and standing-water species increase in numbers and there is a corresponding decline in the numbers of running-water beetles. This unit may be divided into two subunits GP-A7a and GP-A7b, the latter is defined by an increase in cold-adapted species and an almost total loss of any running-water element.”

From the start of GP-A7a the environmental signals become more variable, and, as described above include a constantly higher *Pasture/dung* signal, which is more general than Ponel's coprophagous group. There is general agreement between the systems in terms of woodland and water signals, and the GP-A7a/A7b split is compatible with both BugStat's running water indicators and the MCR values. Although there is a reasonable amount of internal variation in A7a, it is tempting to suggest three subdivisions, as illustrated by B7.1, B7.2 and B7.3 (Figure 6.11):

- B7.1: Mostly distinguishable by its middle sample, 22, which has no species level woodland signal at all, and a dramatically reduced aquatic fauna. It also produces the highest correlation value for the entire sequence, of 0.61 with sample 40. Climatically the unit appears little different from B7.2, although the smaller proportion of standing water species may indicate a different precipitation regime.

B7.2: Similar temperature regime to B7.1, but more constant representation of environments, and an increase in indications of standing water.

B7.3: A slightly warmer period, with greater numbers of taxa and individuals, and a slight increase in woodland habitats.

6.2.6 Conclusions

The intuitive classification of Ponel, based on entomological knowledge, compares closely with the Bugs EcoCodes classification developed independently from a variety of sources. BugStats output is remarkably similar to Ponel's diagrams, considering they are two independently developed systems. Ponel however, uses the number of species and individuals in his plot (closest to the 'raw' outputs in BugStats^{xi}), and the ability to standardize the BugStats output, in terms of percentages of environmental representations of each class by sample sums, allows for some differences in interpretation. As BugStats is intended to be a trans-European system, it inevitably generalizes more than any system built upon single site or regional investigations will do. There is also a significant central-north European bias in BugsCEP as a whole, and southern species may be under-represented and even under defined in terms of their habitat requirements.

Perhaps the most important lesson from this comparison is that whilst raw abundance data are useful for examining apparent changes in numbers representing particular habitats over time, it can be misleading when examining the relative changes over a number of habitat types. Changes in sample diversity may be masked by changes in numbers of taxa and individuals between samples, and the latter may be more a reflection of differential sample size, deposition rate and preservation. Standardization allows us to compensate for these variations without diluting the important habitat signals too much. If used in conjunction with carefully selected indicator species, this can be a powerful tool for interpreting complex faunal changes.

The assignment of species to habitat groups may require further discussion and this is an ongoing process, and such an endeavour is an interesting prospect for future work.

6.3 Fossil Case Study: Early Holocene Environmental and Climate Change at Hemavan, Northern Sweden

Own data contribution: fossil insect data

Other contributors: pollen – Engelmark (1996)
plant macrofossils – Tegby (2004)



Figure 6.12. Panorama photograph of the Hemavan bog taken from the sampling location.

6.3.1 Aims

The lake eroded face of a bog near Hemavan, northern Sweden, was sampled for pollen analyses in the early 1970s by Engelmark (1996). This site was revisited in 2003 by the author of this thesis, and new

^{xi} But not identical, as described in Chapter 4, a BugsCEP taxon may be included in more than one habitat, as may its abundance value.

samples taken close to the original site for the analysis of fossil insects and plant macrofossils. The results are interpreted below with the help of the analytical tools built into BugsCFP.

6.3.2 Site, samples and methods

The Hemavan site lies at 65°50'N, 15°00'E, 450 m a.s.l. in the northern Swedish district of Storuman (Figure 6.13). The sampling location was on the exposed face of a slightly raised bog close to the Ume river, where it is slowly being eroded by wave action from the adjacent lake (Figure 6.12). The rate of erosion appears to have slowed in recent decades, as the location of Engelmark's (1996) sample column was easily identified, despite having been dug in the early 1970s. This, along with the dry surface and obvious ill health of the bog, may be evidence of a falling water table.

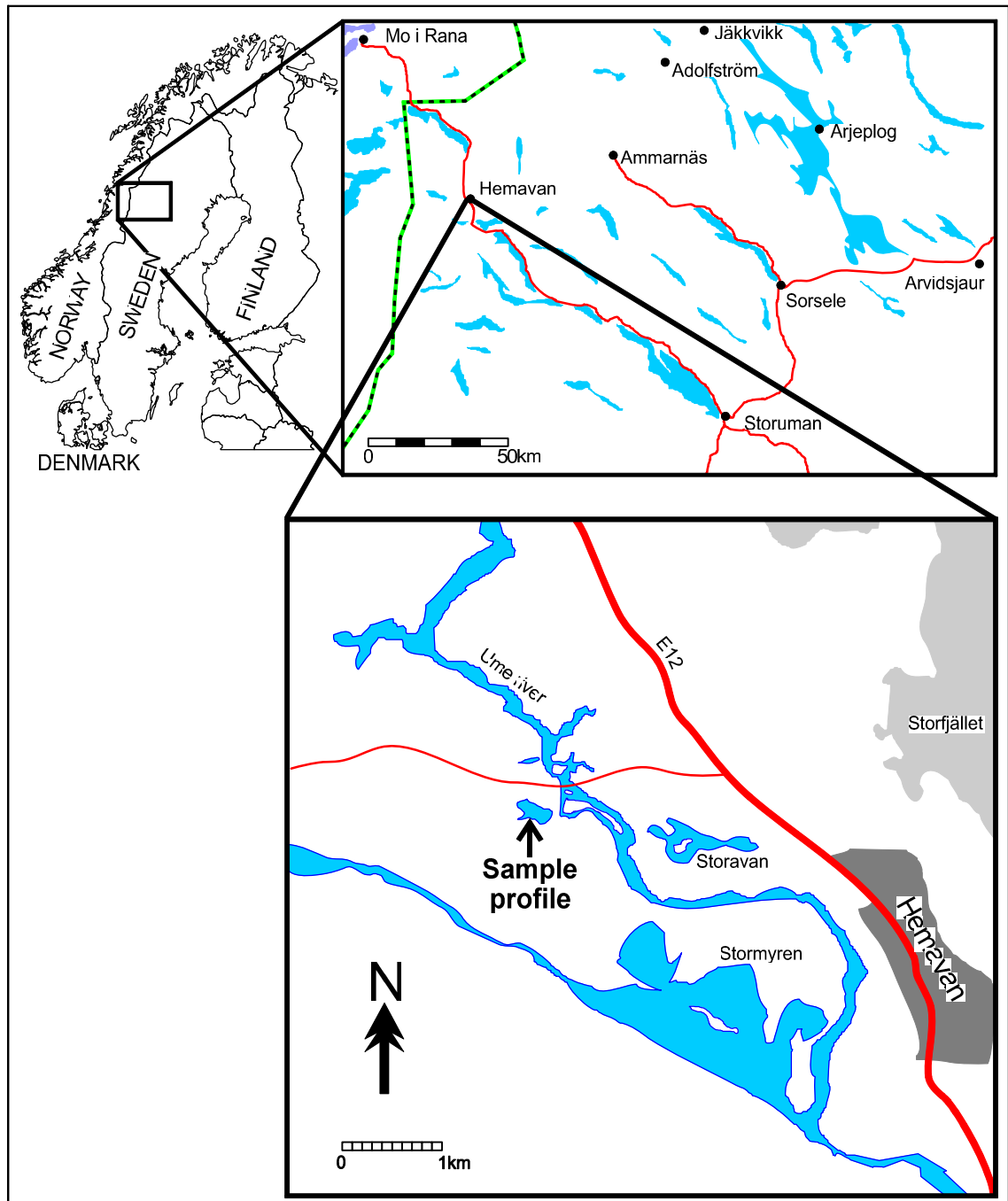


Figure 6.13. Map showing the Hemavan site and location of the sample profile.

Although there are no known archaeological sites in the immediate area of the site, there is considerable evidence of Stone Age activity around the large lake Överuman, some 7 km upstream (Holm, 1991). Previous work has shown that a bog or lake has to be very close to a hunter-gatherer occupation site for any record of the latter's impact on the landscape to be recorded (Hicks, 1993). It was not expected that the effects of the sites surveyed around Överuman would be seen in the samples, but any immediately local site of contemporary age might be visible in terms of faunal changes. It is, however, extremely difficult to differentiate between small scale human impact on the landscape (e.g. dead wood removal, burning) and natural environmental change.



Figure 6.14. Photograph of the sampling location, with remains of Engelmark (1996) section in the foreground on the left. Paul Buckland is documenting the vegetation (and simuliids) in the background.

It was decided to sample from the same profile as Engelmark (1996) (Figure 6.14), both to increase the comparability of results and to reduce damage to the bog. The section was cleaned, and a total of 30 samples of approximately 5 litres each were extracted, in 5 cm slices, covering a depth of 160 cm (Figure 6.15). The top 50 cm of peat were avoided due to obvious desiccation, which suggested that preservation would be poor. Extraction of the lowest 30 cm of sediment proved difficult due to ground water and arm length, and so the sample depths are less reliable for these samples (132 to 160 cm). Samples 130-135cm and 132-135+cm are from the base of the peat and the top of the clay respectively. Sampling in this way, rather than an even 5 cm block, should prevent the mixing of faunas from different sedimentological and environmental regimes. The sample column was approximately correlated with that of Engelmark (1996) by use of his raw data and distinguishable horizons (a dark humified band, the peat-clay interface) within the sediment (Figure 6.15), and the approximate depth from the peat surface.

Ten samples were chosen for analysis, to represent a reasonable chronological depth whilst focusing on the clay-peat transition. Unfortunately, time constraints prevented the analysis of further samples,

but they are in cold storage for future work. Sub-samples were taken for future reference (e.g. geochemistry), and the sediments described according to Troels-Smith's (Aaby & Berglund, 1986) classification for unconsolidated sediments (Table 6.7). Samples were disaggregated in warm water and washed through a 300 μm sieve. A few of the less humified samples swelled enormously (up to 200 % in volume) and were treated as two samples sieved at 300 μm and 2 mm respectively (the smaller catching the drainage of the larger). The insect faunas were examined separately from these and accordingly labelled as 'big' and 'small'. All samples were paraffin floated three times, washed in detergent, stored in ethanol and then examined under a binocular microscope. Species were identified by the use of reference literature and the modern reference collection at Manchester Natural history Museum (UK), by the author, with the assistance of Paul Buckland.

Abundance data was fed into BugsCEP as the site "Hemavan", and EcoFig and MCR plots produced. Plant macro fossils were also identified from number of samples by Ida Tegby (2004), and the results are discussed in relation to the insect data below.

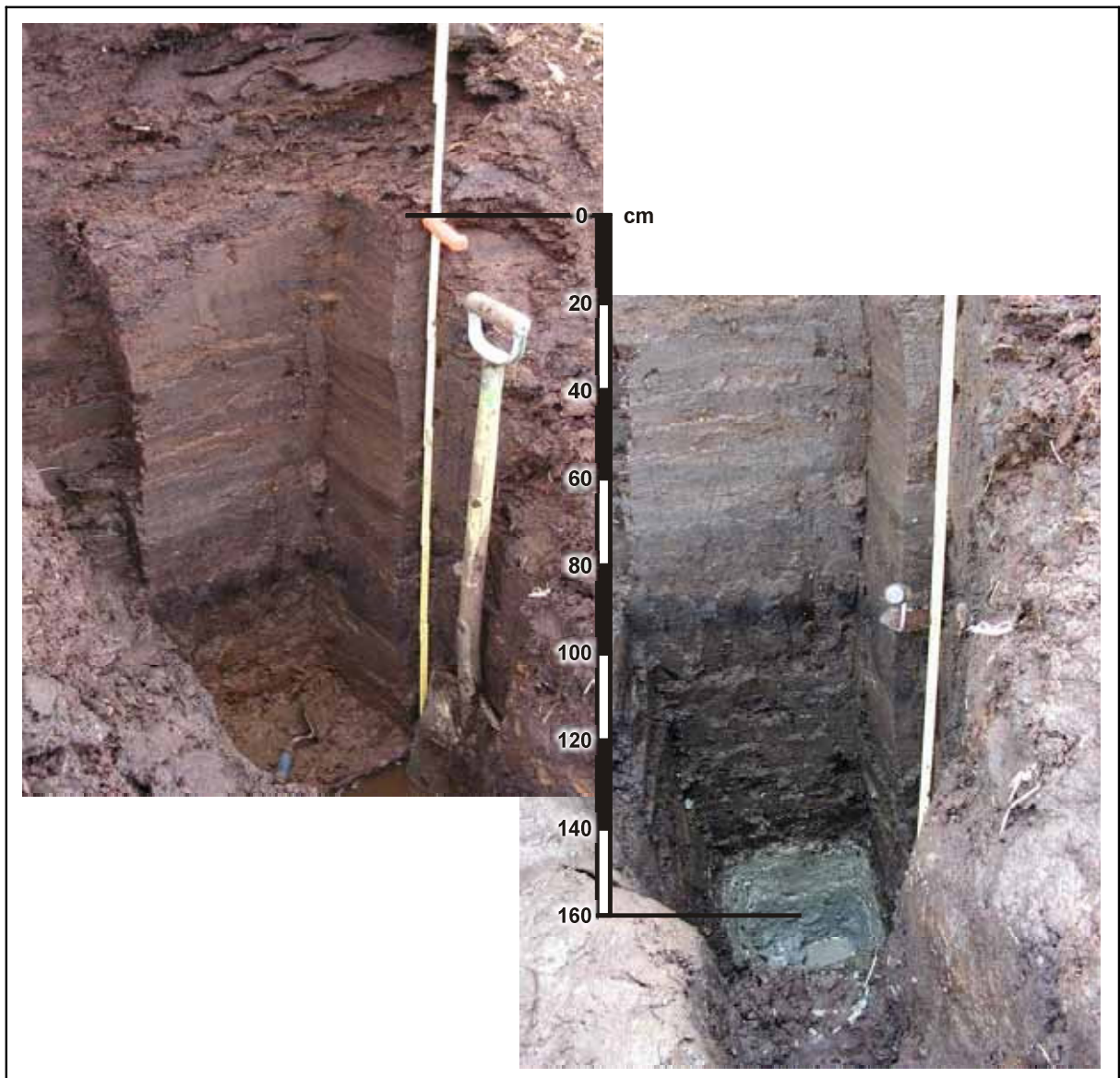


Figure 6.15. Photograph showing the sampling pit at two stages of excavation. The scale is approximate and for illustration only. A dark, more humified band can be seen at c. 100 cm, and the peat-clay transition is visible at about 135 cm.

Table 6.7. Hemavan – processed sample depths and descriptions. Sample depths are in cm.

Bottom depth	Top depth	Processed size (L)	Size >300 (ml)	Flot size (ml)	Troels-Smith	Description
55	60	5	5500	75	Tb ¹ 4Th ¹ +Tl ¹ +	Moderately well stratified moss peat, some twigs and plant bits, very poorly humified, some rhizomes/roots (vertical).
60	65	6.5	5250	300	Tl ¹ 1Th ¹ 2Dh1	Moderately stratified, fibrous peat, many twigs, a few roots, some large twigs. Flot was efloated and sorted as fine and coarse parts.
65	70					
70	75					
75	80					
80	85					
85	90	7	7000	50	Th ² 1Dh2Dg1	Moderately stratified, fine fibrous peat, some many rhizomes, very few other roots (4th float made).
90	95					
95	100					
100	105					
105	110					
110	115	7	7500	100	Th ¹ 2Dh2	Well stratified, poorly humified peat, some roots.
115	120	5.5	7500	100	Th ¹ 3Dh1	Well stratified, poorly humified peat, very few twigs.
120	125	1+5	5000	60	Tl ¹ +Th ² 1Dh2Dg1	Poor-moderately humified peat, a few twigs ~fibrous (1 litre subsampled for unsuccessful NOH ₃ disaggregation test; 4th float made).
125	130	5	3500	100	Tb ² 1Th ¹ 2Tl ¹ 1	Poor-moderately humified peat, lenses of more humified peat. Some twigs and roots.
130	135	4.5	2000	50	Tb ³ 3Th ² 1+lenses	Moderately humified peat with lenses of less humified peat, and silt lenses. Uneven base to peat.
132	135+	4	700	50	95 %: As1Ag3Th ² + 5 %: lenses Tb ³ 3Th ² 1	Grey-brown clayey silt, many roots. Uneven top of clay.
135+	140	4	780	25	As1Ag3Dg ² +Dh ² +	Grey-brown clayey silt, some roots, fine organic fibres.
145	160	5	800	35	As1Ag3Dg ² +Dh ² +	Grey-brown clayey silt, some roots/reeds, fine organic material.

6.3.3 Results

Species abundances were generally poor, despite the large sample volumes (Table 6.8). The maximum sample abundance was 56 MNI (Minimum Number of Individuals), in the basal peat sample 130-135cm, and the minimum of two MNI occurred in the sample 135+-140cm. The most species rich sample was 60-65BIG (large float fraction), and this sample would most certainly have proved to have been exceptionally rich had there been time to identify the remaining fine float fraction.

Only standardized EcoFigs were produced (Figure 6.16), as the low abundance values in several samples would lead to un-proportional visual representation of the habitats of the species found.

Engelmark's (1996) pollen data are reproduced here in percentage form, along with selected parts of Tegby's (2004) plant macrofossil data for comparison. Although the numbers were small, enough MCR beetle species were present to allow for a rudimentary climate reconstruction (Figure 6.17) with some interesting results which are discussed below.

Table 6.8. Beetle species list from Hemavan (continued on next page).

Taxon	55-60Pt2	60-65BIG	110-115	115-120	120-125	125-130	130-135	132-135+	135+-140	145-160
<i>Loricera pilicomis</i> (F.)	1									
<i>Bembidion</i> sp.										1
<i>Patrobus septentrionis</i> (Dej.)						1				
<i>Patrobus assimilis</i> Chaud.				1			1			
<i>Patrobus</i> sp.		1								
<i>Pterostichus diligens</i> (Strm.)	1	1					3			
<i>Pterostichus strenuus/diligens</i> (Panz.)/(Strm.)				1						
<i>Pterostichus nigrita/rhaeticus</i> (Payk.)/Heer							1			
<i>Agonum piceum</i> (L.)		1								
<i>Agonum gracile</i> Strm.	1	1								
<i>Agonum fuliginosum</i> (Panz.)		1	1			1				
<i>Hydroporus memnonius</i> Nic.					1	2	4			
<i>Hydroporus</i> sp.		2								
<i>Hydraena britteni/riparia</i> Joy/Kug.								1		
<i>Cercyon</i> sp.							1			
<i>Leiodidae</i> indet.		1								
<i>Acrulia inflata</i> (Gyll.)		1								
<i>Olophrum consimile</i> (Gyll.)		5			1	3	3			1
<i>Olophrum rotundicolle</i> (Sahl.)	1						2			
<i>Olophrum</i> sp.		1								
<i>Eucnecosum brachypterum</i> grp.	5	2								1
<i>Acidota crenata</i> (F.)	1	1					1			
<i>Acidota cruentata</i> (Mann.)	1									
<i>Acidota quadrata</i> (Zett.)										1
<i>Anthophagus alpinus</i> (Payk.)		1								
<i>Anthophagus omalinus</i> Zett.	1									
<i>Omalinae</i> indet.		2					2			
<i>Bledius</i> sp.									1	
<i>Stenus</i> spp.	4	3			2	2	1			
<i>Euaesthetus bipunctatus</i> (Ljungh)		1	1	1						
<i>Lathrobium</i> spp.		6	1	2	3	6	8	1		
<i>Ochtheophilum fracticorne</i> (Payk.)		2	1		1	1				
<i>Philonthus</i> sp.	2	1					3			
<i>Platydracus pubescens</i> (Deg.)	1									
<i>Staphylinus erythropterus</i> L.						1				
<i>Quedius</i> spp.		4			2	1	2			
<i>Mycetoporus splendidus</i> (Grav.)		1								
<i>Tachyporus</i> sp.							1			
<i>Tachinus signatus</i> Grav.										1
<i>Tachinus</i> sp.					1					
<i>Aleocharinae</i> indet.	2	3					2			
<i>Bryaxis bulbifer</i> (Reich.)				1						
<i>Bryaxis</i> sp.	2	1	4	4	2	3				

Taxon	55-60Pt2	60-65BIG	110-115	115-120	120-125	125-130	130-135	132-135+	135+-140	145-160
<i>Pselaphaulax dresdensis</i> Hbst.							1			
<i>Rhagonycha testacea/femoralis</i> (L.)/(Brul.)							1			
<i>Rhagonycha</i> sp.							1			
<i>Hypnoidus rivularius</i> (Gyll.)										1
<i>Scirtidae</i> indet.	1			1	2					
<i>Dryops</i> sp.										1
<i>Cytilus sericeus</i> (Forst.)					2	6	4			
<i>Phratora</i> sp.						1				1
<i>Crepidodera fulvicornis</i> (F.)		1								
<i>Chaetocnema</i> sp.	1				1					
<i>Curculionidae</i> indet.							1			
<i>Otiorhynchus nodosus</i> (Müll.)							1			
<i>Bagous</i> sp.			1	2						
<i>Dorytomus taeniatus</i> (F.)								1		
<i>Ellescus bipunctatus</i> (L.)									1	
<i>Limnobaris dolorosa</i> (Goez.)			1	1	1	13	11			
<i>Ceutorhynchinae</i> indet.						1	1			
<i>Rhynchaenus testaceus</i> (Müll.)	1	1								

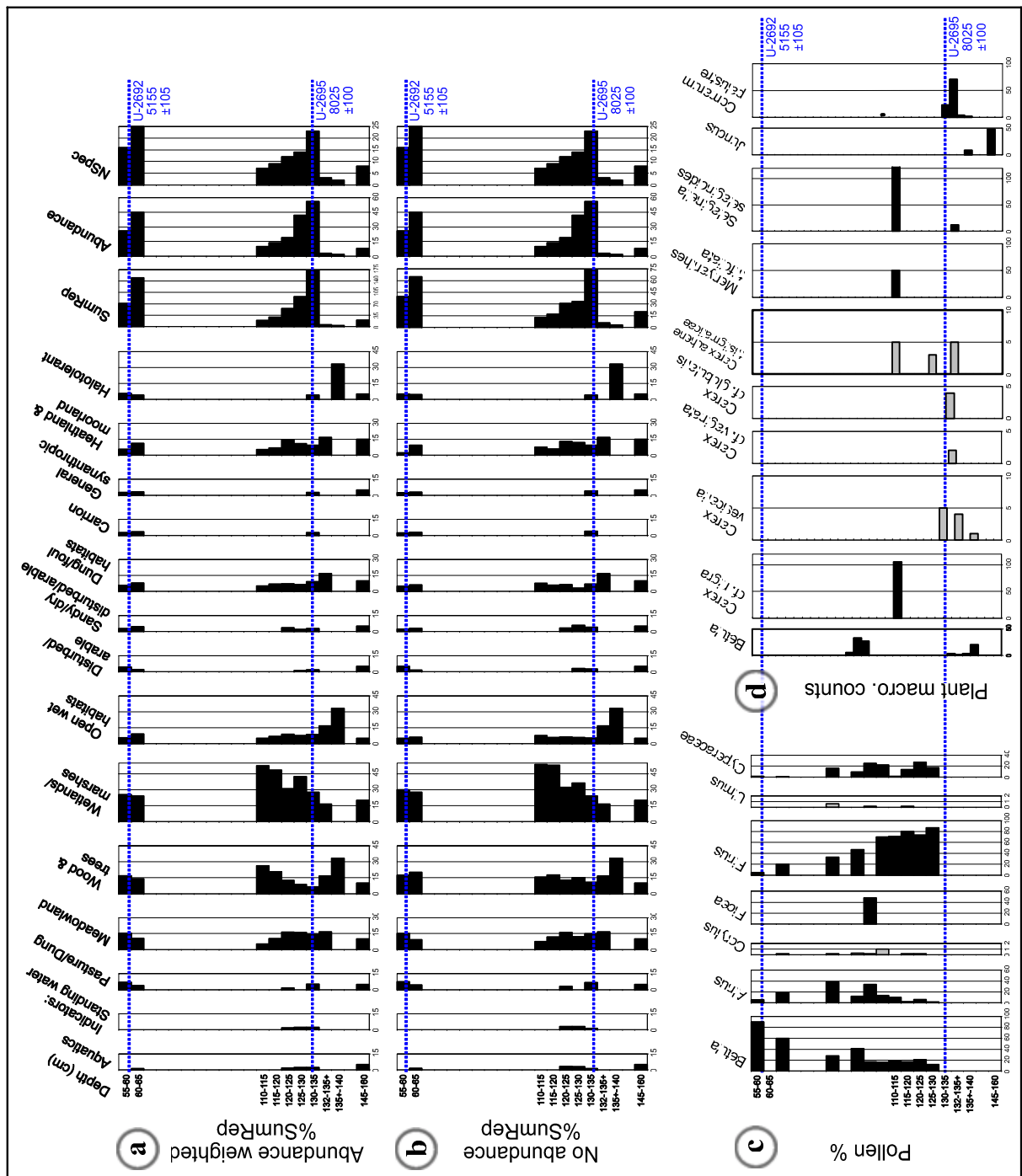


Figure 6.16. Bugs EcoFigs and other biological proxies for Hemavan. Standardized beetle reconstructions with (a) abundance weighting and (b) taxa only. Diagram (c) shows summary pollen percentage data, and (d) raw plant macrofossil counts. Radiocarbon dates are uncalibrated, and transferred by stratigraphic correlation.

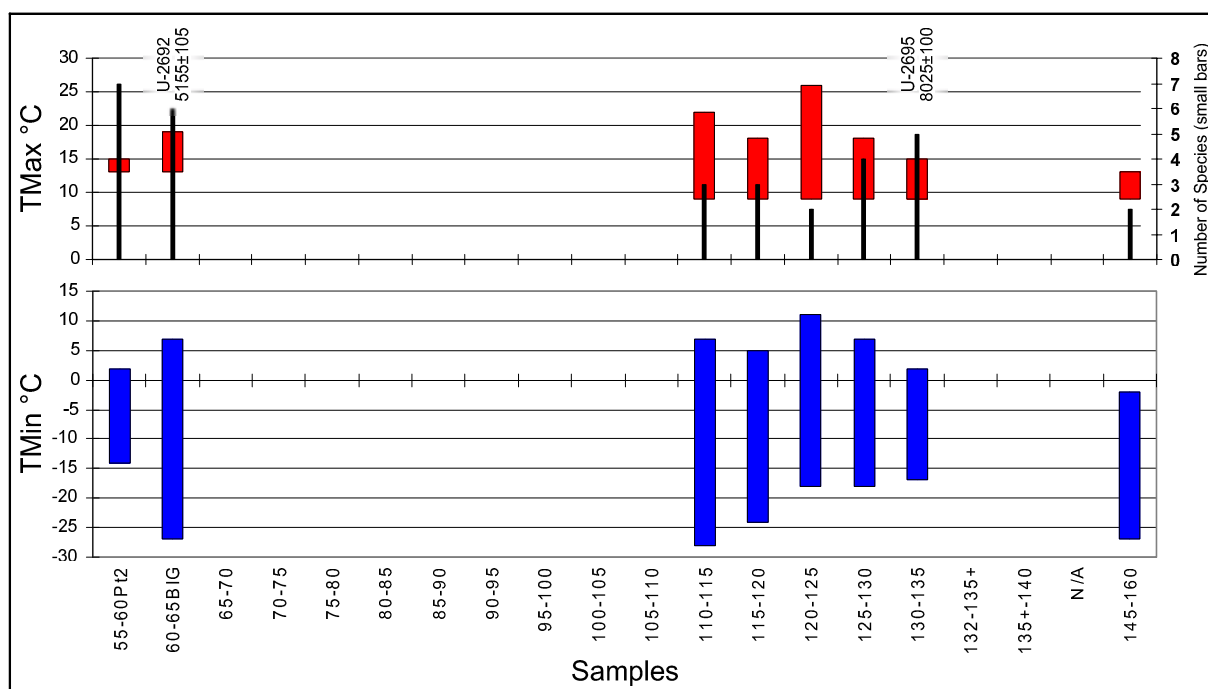


Figure 6.17. MCR reconstruction of palaeotemperatures from Hemavan. Uncalibrated ^{14}C dates are shown on the diagram; 1 σ calibrated ranges U-2692: 5122-6184 BP and U-2695: 8599-9243 BP (Oxcal version 4, Bronk Ramsey, 1995). Present day temperatures: TMax: 8 to 10°C; TMin: -15 to -12°C (SMHI, 2005)

6.3.4 Discussion

As is often the case where sample columns cross sediment boundaries, there is considerable difference in the species richness and total abundance between samples. This necessitates the standardization of EcoCode counts to compensate for these variations, so that samples with higher diversity do not automatically gain stronger habitat indications. Where the sediment type is the same, however, it could be argued that the insect diversity could be a proxy for bog growth rate – a fast growing bog accumulating less individuals per unit time than a slow growing one. This assumes a constant rate of ‘capture’, which is difficult to prove without independent evidence from another deposit in the area.

The beetle faunas appear to depict an initial picture of a lake overgrowing into a bog. Unfortunately the number of species (2) and individuals (2) in samples 135+-140 and 132-135+ are too low for this to be realistically assumed. There is, in fact, very little indication of open water in the sequence, and the five most prominent habitat signals (*Meadowland*, *Wood & trees*, *Wetlands/marshes*, *Open wet habitats* and *Heathland & moorland*) are those that would be expected from a peat bog, with some small pools and wet mud on the surface, surrounded by woodland. There is strong evidence for the presence of standing water, in the form of the Bugs EcoCode indicator species *Hydroporus memnonius* Nic. (Nilsson & Holmen, 1995). The *Dung/foul* habitats implied in all samples, are almost all the result of generic level identifications of Staphylinid beetles of the genera *Lathrobium*, *Omalium*, *Philonthus*, along with *Cercyon* and *Aleocharinae*. The only individual representing this habitat that could be identified to species was the predatory rove beetle *Tachinus rufipes* (L.), which is as much at home in dung or decaying organic matter as in wetter grasslands and bogs (Andersen *et al.*, 1990; Koch, 1989). By far the dominant habitat indicated is that of *Wetland/marshes*, which would be expected for a peat bog. If one disregards samples 135+-140 and 132-135+ due to their low numbers, one can also see an indication of a gradual increase of woodland and trees around the bog.

There appears to be contradictory evidence when comparing the BugStats output with the pollen percentage data. The pollen data suggest a woodland landscape, initially dominated by pine just after 8 000 ^{14}C BP, gradually being replaced by birch, which totally dominates the pollen flora at 5 155 ^{14}C BP. This may reflect differing areas of representation of the insect fauna and the pollen

flora. Pollen is more easily wind transported than insects, with pine pollen being the extreme example. Many insects are also more inclined to directed travel, in that they will actively search for favourable habitat, rather than being passively borne on the wind. This increases the probability that an insect found in a trap in a particular environment will, by its own volition, have intended to be there and thus represent the environment. With this reasoning one can suggest, in this context, using the pollen to paint a picture of the wider surroundings, and the beetles and plant macrofossils to reconstruct the immediate bog surface, and to a lesser extent the immediate surroundings.

The plant macrofossil data shows early indications of bog/wetland growth in the form of *Carex* spp., *Comarum palustre* L., *Menyanthes trifoliata* L. and *Selaginella selaginoides* (L.). Birch is indicated, and most probably growing at the edges of the bog. These data support the local environment described by the insect data, and complement the more regional signal from the pollen data. Treeline megafossil evidence from the region (Kullman, 1992), although difficult to interpret in terms of populations, are broadly supported by the pollen evidence of Engelman (1996) if one assumes that the conditions for a heightened species treeline also lead to a relative increase in the pollen abundance of the species at lower altitudes. More high altitude beetle studies are required to assess the ability of beetle faunas to reflect changes in treeline vegetation.

6.3.5 Evidence for early Holocene climate change

The lowest insect sample (145-160cm, >9 243 Cal. BP) may suggest a slightly colder thermal regime than the higher samples, somewhat similar to the present day temperatures at Hemavan. Although the range of possible temperatures overlaps the majority of the samples (the exceptions being the highest processed samples from 55-65 cm), the fact that the upper limits of both TMax and TMin are lower than in any other samples may be significant. This result is somewhat steered by the presence of *Acidota quadrata* (Zett.) which has a particularly narrow TMax span of 9 to 13°C. Using the 'Predict' function in BugsMCR, it can be seen that the only other species in the MCR database that could fit within this range is the cold tolerant but more hygrophilous *Elaphrus lapponicus* Gyll. Both species are known from Late Glacial samples from sites in the UK (e.g. West Bromwich (Osborne, 1980); Red Moss (Ashworth, 1972)), Denmark (Nørre Lyngby, (Coope & Böcher, 2000)) and Sweden (e.g. Körslättamossen (Hammarlund & Lcmdahl, 1994); Björkcröds Moss (Lcmdahl, 1988))^{xii}. The present day geographical distributions of both species in Sweden are very similar, and show a distinct northern preference (Gustafsson, 2005), suggesting that the reason for the presence of only one of them in the sample may not be explainable in terms of distributional factors. In which case, one could look to ecological factors and taphonomy (including chance) to explain the absence of *E. lapponicus* from a sample that it theoretically could populate. It could be that the Early Holocene climate of Hemavan was too dry for this species. Although this is a potential explanation, the small number of individuals in the sample (8) give more weight to an explanation in terms of a low probability of incorporation into the sample, and the suggestion that a much larger sample would be needed to assess the hypothesis.

Table 6.9. Thermal limits for species in Hemavan bottom sample 145-160cm. See Chapter 5 for explanation of variables.

Species	TMaxLo	TMaxHi	TMinLo	TMinHi	TRangeLo	TRangeHi
<i>Acidota quadrata</i> (Zett.)	9	13	-30	-2	15	39
<i>Tachinus signatus</i> Grav.	9	27	-27	15	7	36

The only other MCR species present in the sample, *Tachinus signatus* Grav. is a cold tolerant but significantly more eurythermal species (Table 6.9), currently known from the whole of Sweden, which may be living towards the lower limits of its thermal tolerance in this sample. In contrast to *A. quadrata* there are 235 species in the database which could survive within the TMax limits of *T.*

^{xii} This is not an exhaustive list, consult BugsCEP for further sites.

signatus. Koch (1989-92) classifies this species^{xiii} as ubiquitous (Habitat range: Ub) and saprophilous (Food type: sa; in decaying materials), and Good & Giller (1991) record it as a predator on the larvae of other Coleoptera, Diptera and Collembola. These are characteristics which would give the species a good chance of survival in a recently deglaciated landscape.

Although the samples from 110-135 cm provide temperature reconstructions which overlap those from the basal clay sample (145-160 cm), the samples at 55-60 cm and 60-65 cm suggest mean July temperatures of 13-15°C and 13-19°C, the lower limits of which represent a regime some 3-5°C warmer than the present day. Dated to 5122-6184 Cal. BP, this is only slightly later than the expected early Holocene warm period suggested by other proxies for northern Sweden (e.g. Bigler *et al.*, 2002). Analysis of the remaining samples is necessary to investigate as to whether this is an anomaly, or part of a pattern reflected in other mid-Holocene samples from Hemavan, such as the development of more oceanic conditions. There is currently insufficient evidence in the beetles to assess the evidence for climatic change presented by the megafossil data of Kullman (1992).

6.3.6 Conclusions

The environmental reconstruction from Hemavan give a picture of Early Holocene bog growth which is compatible with current understanding of the post-Glacial development of the region, and indicated the complementary nature of palaeoentomological, plant macrofossil and palynological evidence. The reconstruction temperatures are compatible with those derived from other proxies from northern Sweden (e.g. Rosén *et al.*, 2001), although much of the Hemavan sequence is yet to be analysed. More samples will need to be examined in order to produce a fuller picture of Mid-Holocene environmental and climate change in the region, and deposits from other bogs and lakes in the area should be examined to enhance the understanding of a poorly researched region.

6.4 Fossil Case Study: Two 'Wells' at the Archaeological Site Lockarp 7B, Sweden.

Own data contribution: fossil insect data

Site reference: Eliasson & Kishonti (2003)

6.4.1 Aims and introduction

The aim of this study was to examine the beetle fauna of an archaeological feature described as a well through the BugsCEP software, and create a reconstruction of the environment represented by the species present. The fossil insects from archaeological well deposits of different ages have been studied by a number of authors (Late Neolithic: Schelvis, 1989; Bronze Age: Masfield, 2003; Osborne 1969, 1989; Iron Age: Antipina *et al.*, 1991; Hellqvist, 1999; Hellqvist & Lemdahl, 1996), and especially from Roman well deposits (Alvey, 1976; Buckland, 1980 & 1986; Coope & Osborne, 1968; Girling, 1989; Hakbijl *et al.*, 1989; Kenward *et al.*, 1986; Lentacker *et al.*, 1992; Mertens *et al.*, 1986; Osborne, 1975; Simpson, 2001; Sudell, 1990; and others). Wells have been compared with giant pitfall traps (Buckland, 2000; Hellqvist, 1997), although their location will be critical to their trap effectiveness. Covered or indoor wells, for example will most probably produce much poorer faunas than open or outdoor ones.

The interpretation of wells is generally difficult, and especially so where the archaeological interpretation is problematic. There is a tendency, in Swedish archaeology at least, to interpret almost every significant excavated filled depression as a well, even before palaeoecological analysis have been undertaken. Such an *a priori* hypothesis is only acceptable as long as it does not interfere with

^{xiii} See Chapter 4 for more information on Koch's ecology codes.

interpretation, especially if the insects and plant macrofossils provide evidence to the contrary. So called ‘wells’ equally often turn out to have been dew ponds, animal drinking troughs or cisterns, where the water quality was almost certainly unfit for human consumption on the evidence of the insects (e.g. Jaques *et al.*, 2000), although by the time accumulation had begun in the feature it may have ceased to be a water source.

The samples analyzed here form part of a large archaeological project connected to the construction of a major new roadway system around Malmö, Sweden (Eliasson & Kishonti, 2003). A number of other analyses, including plant macrofossils, snails and soil chemistry were undertaken on the samples by the Environmental Archaeology Lab at Umeå, Sweden, summary reports for which can be found in Eliasson & Kishonti (2003). A synthesis of the environmental evidence will be available in a forthcoming publication (Engelmark & Linderholm, *in prep.*).

6.4.2 Methods

The two sets of samples interpreted here were submitted to the Environmental Archaeology Lab in Umeå as coming from two wells, numbered 14495 and 26551. Both features were sampled with kubiena box columns from the excavated profiles, and the stratigraphy of both features is shown in Figure 6.18 and Figure 6.19. Although sample size was small it was possible to retrieve insect remains from the lower part of the column, where preservation was sufficient for identification. These samples were washed through a 300 µm sieve and examined under a binocular microscope. Insect remains were extracted and identified by the author of this thesis, under the guidance of Paul Buckland, with reference to identification keys and modern reference collections. Environmental interpretation was undertaken with the help of the BugsCEP software, and reconstruction diagrams were produced using the BugStats component (Figure 6.20).

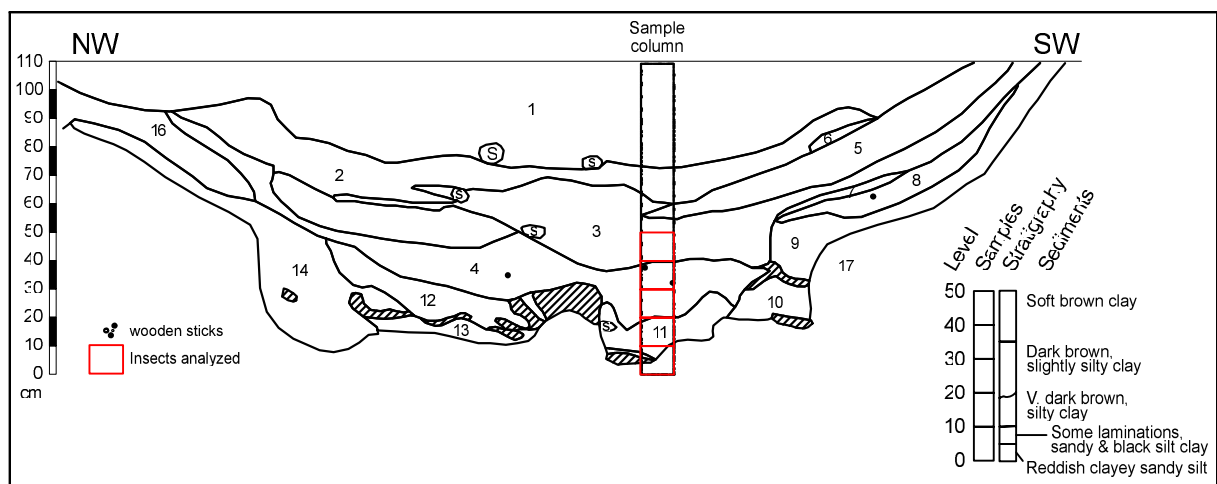


Figure 6.18. Stratigraphy and sample locations in feature 14495, Lockarp 7B. Stratigraphy provided by Johan Linderholm; archaeological sediment descriptions can be found in Eliasson & Kishonti, (2003).

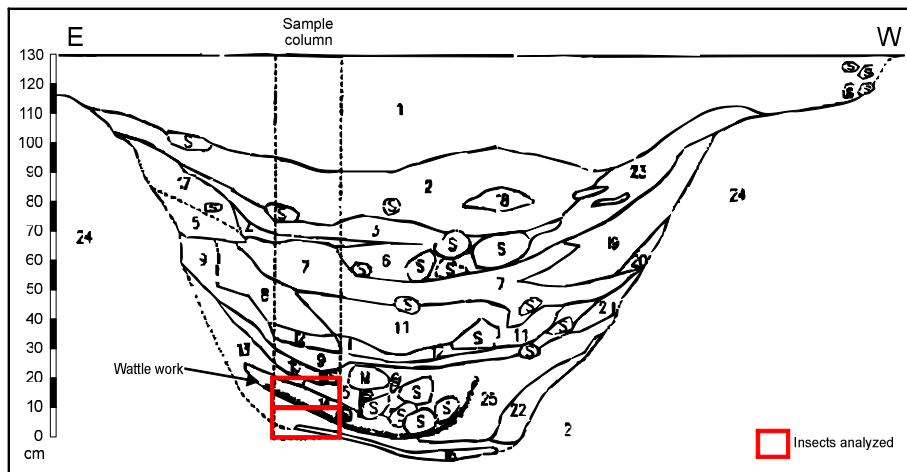


Figure 6.19. Stratigraphy of feature 26551, Lockarp 7B. Insects were only preserved in the bottom 20 cm of the sequence. Stratigraphy provided by Johan Linderholm; archaeological sediment descriptions can be found in Eliasson & Kishonti, (2003).

6.4.3 Results and discussion

A total of 35 taxa were identified from the five samples from feature 14495 (Table 6.10), and 40 from feature 26551's two samples (Table 6.11). Species abundances were low, with a maximum MNI of 4 for any taxon. Species richness was generally low in all samples, with sample 10-20 from feature 26551 producing the highest number of taxa. Small sample size and variable preservation are responsible for these low numbers. Only %SumRep outputs were produced, as the use of absolute abundances where the numbers are so low would produce the appearance of grossly exaggerated signals from the more plentiful taxa in a raw abundance weighted diagram. A raw taxa (no abundance) diagram could also be misleading in that the species richness of the samples varies considerably.

Table 6.10. Beetle species from Lockarp 7B feature 14495.

Taxa	S0-10	S10-20	S20-30	S30-40	S40-50
<i>Dyschirius</i> sp.		1			
<i>Bembidion properans</i> Steph.				1	
<i>Pterostichus vernalis</i> (Panz.)				1	
<i>Hydraena</i> sp.				1	
<i>Helophorus brevipalpis</i> Bed.			3	1	
<i>Helophorus brevipalpis</i> grp.			4		
<i>Laccobius</i> sp.				1	
<i>Silpha</i> sp.					1
<i>Anotylus rugosus</i> (F.)				1	
<i>Anotylus nitidulus</i> (Grav.)			1		
<i>Platystethus nodifrons</i> (Mann.)	1	2	1		
<i>Platystethus nitens</i> (Sahl.)				1	
<i>Stenus</i> sp.		1			
<i>Xantholinus</i> sp.		1			
<i>Dryops</i> sp.			1		
<i>Geotrupes stercorarius</i> (L.)			1		
<i>Onthophagus joannae</i> Golj.				1	
<i>Oxyomus sylvestris</i> (Scop.)					1
<i>Aphodius sticticus</i> (Panz.)		1			
<i>Aphodius obliterated</i> Panz.				3	
<i>Aphodius contaminatus</i> (Hbst.)	1				
<i>Aphodius sphacelatus</i> (Panz.)			2		
<i>Aphodius prodromus</i> (Brahm)			2		
<i>Aphodius foetidus</i> (Hbst.)				1	
<i>Aphodius granarius</i> (L.)		2	2		
<i>Aphodius</i> sp.	1		2	1	
<i>Aphodius</i> spp.				3	2
<i>Longitarsus</i> sp.	1		2		
<i>Ochrosis ventralis</i> (Ill.)	1				
<i>Chaetocnema</i> sp.		1			
<i>Psylliodes affinis</i> (Payk.)		2	2		
<i>Psylliodes</i> sp.				1	1
<i>Sitona</i> sp.			1		
<i>Dorytomus</i> sp.			1		
<i>Ceutorhynchus</i> sp.			1		

Table 6.11. Beetle species from Lockarp 7B feature 26551.

Taxa	S0-10	S10-20
<i>Carabus violaceus</i> L.	1	1
<i>Bembidion properans</i> (Steph.)		2
<i>Pterostichus strenuus</i> (Panz.)		1
<i>Pterostichus niger</i> (Schall.)		1
<i>Calathus fuscipes</i> (Goeze)	1	1
<i>Hydroporus</i> spp.		3
<i>Ochthebius</i> sp.		1
<i>Sphaeridium bipustulatum</i> F.		1
<i>Sphaeridium lunatum</i> F.	1	2
<i>Cercyon melanocephalus</i> (L.)		1
<i>Cercyon</i> sp.	1	
<i>Megasternum obscurum</i> (Marsham)		2
<i>Manda mandibularis</i> (Gyll.)		1
<i>Aploderus caelatus</i> (Grav.)		1
<i>Aploderus</i> sp.	1	
<i>Anotylus rugosus</i> (F.)		2
<i>Anotylus nitidulus</i> (Grav.)		2
<i>Platystethus cornutus</i> (Grav.)		3
<i>Platystethus nodifrons</i> Mann.	1	2
<i>Platystethus nitens</i> (Sahl.)	1	4
<i>Stenus</i> sp.		1
<i>Philonthus</i> sp.	1	1
<i>Quedius</i> sp.		1
<i>Aleocharinae</i> indet.	1	3
<i>Athous haemorrhoidalis</i> (F.)		1
<i>Dryops</i> spp.		4
<i>Enicmus</i> sp.		1
<i>Corticaria</i> sp.	1	2
<i>Scymnus frontalis</i> (F.)	1	
<i>Scymnus</i> (s.l.) sp.		1
<i>Anthicus</i> (s.l.) sp.		1
<i>Aphodius erraticus</i> (L.)		1
<i>Aphodius rufipes</i> (L.)		1
<i>Aphodius contaminatus</i> (Hbst.)		2
<i>Aphodius foetidus</i> (Hbst.)		1
<i>Aphodius</i> sp.		1
<i>Aphodius</i> spp.		2
<i>Phyllotreta nemorum</i> (L.)		1
<i>Aphthona</i> sp.	1	
<i>Longitarsus</i> sp.	1	
<i>Longitarsus</i> spp.		3
<i>Chaetocnema concinna</i> (Marsham)	2	
<i>Psylliodes affinis</i> (Payk.)		1
<i>Psylliodes</i> sp.	1	
<i>Notaris acridulus</i> (L.)		1
<i>Tychius</i> sp.		1
<i>Salda</i> sp.		1

6.4.3.1 Feature 14495

The low abundances are reflected in the little difference between the abundance weighted (Figure 6.20a) and no abundance (Figure 6.20b) outputs from feature 14495. A slightly higher aquatic signal was derived from the abundance weighted reconstruction of the 20-30 cm level, along with a few minor variations in the other signals, but the broad patterns are the same. The most immediately obvious feature is the *Aquatics* signal between 20-40 cm, which is mirrored with a drop in *Meadowland* habitats and a slight indication of *Open wet habitats*. In a set of samples with such low diversity there is a slight chance that this is an artefact, as the surrounding samples have fewer species and individuals and so probability dictates that they are less likely to reflect as many environments as those with higher numbers. Since this feature has been archaeologically interpreted as a well, however, it is reasonable to assume some truth in the signal. It could be that these two samples represent the only true well phase in the sequence, and that the other samples represent construction and collapse phases. Alternatively, and this could be supported by the increased diversity, these two samples represent an open well phase where more beetles accumulated in the well.

There is a relatively strong dung signal throughout the sequence, especially in the bottom 40 cm where it is represented by indicator species. These species, which include *Geotrupes stercorarius* (L.), *Aphodius contaminatus* (Hbst.), *Aphodius sphacelatus* (Panz.), *Aphodius prodromus* (Brahm) and *Onthophagus joannae* Goljan, are highly dependant on animal dung for their survival and reproduction, and thus their presence in samples is as near to 100 % an indication as science can provide^{xiv} (Geoffrey Lemdahl, *pers. comms*). Some of them are also specific to particular substrate materials, and can tell more about the area around the well than just the fact that there were very probably large herbivores there. *O. joannae* is a good indication of sandy or calcareous soils (Duff, 1993; Jessop, 1986).

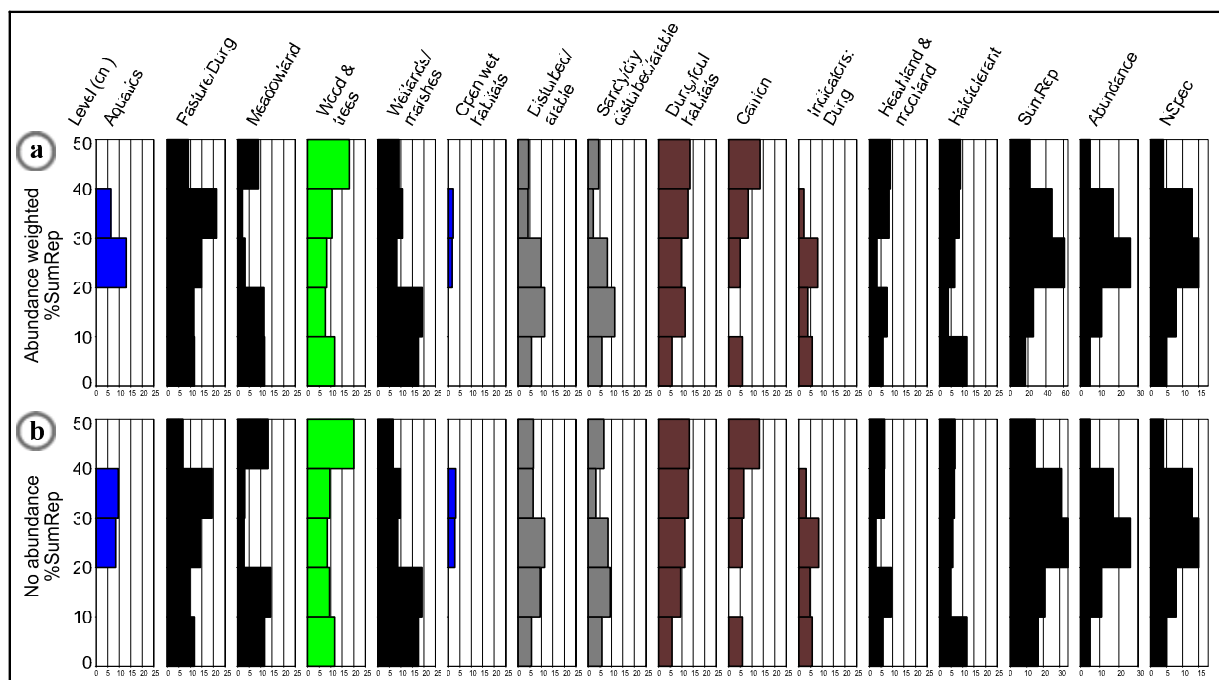


Figure 6.20. BugStats output for Lockarp 7B feature 14495. Both diagrams are standardized, showing (a) abundance weighted and (b) taxa only results.

^{xiv} Gunnar Gustavsson provided help with the indicator species list. *A. sphacelatus* may not necessarily belong in the indicator class (as suggested by Koch 1989 and others), as a number of sources indicate that it is often found in decaying vegetation as well as dung (Duff, 1993; Jessop, 1986; Landin, 1961; Machatschke 1969). Geographical variation in stenotopy creates classification problems (as described in Chapter 4).

The *Dung/foul habitats* class caters for the fact that a number of species are equally happy in other decaying matter as well as dung, and the *Carrion* category has some overlap with this. These are good indications of what would be considered as a farmyard environment today, but in fact, would probably be fairly typical of any dwelling site or settlement before the early modern period, when a clearer separation between human and animal occupation areas began. There appears to be a steady increase in indications of pasture (*Pasture/Dung*) from the bottom of the sequence, provided by an increasing proportion of *Aphodius* species in the samples, although identifying such trends through samples with so few individuals is dangerous.

The *Halotolerant* signal, which is more or less constant after an initial peak, is entirely the result of generic level identifications of the ground beetles *Dyschirius* sp., dung beetles *Aphodius* sp(p), and flea beetles *Longitarsus* sp.. In this case it should probably be ignored, as there are few too individuals involved for the signal to be probable.

6.4.3.2 Feature 26551

As can be seen from Figure 6.21, the two samples from this feature have number of similarities with samples S10-20 and S20-30 from feature 14495 (Figure 6.20), which could be an indication that they both represent the transition from primary sediments to water deposited layers. The lower sample has no indication of *Aquatics*, but a reasonable indication of *Wetlands/marshes*, suggesting some wetland vegetated areas in the surroundings, but no open water. Sample S10-20, on the other hand, shows a definite water signal in the presence of water beetles of the genera *Hydroporus* and *Ochthebius*. There is a *Halotolerant* signal in both samples, suggesting saline environments. Closer examination of the fauna reveals, as above, that this is the result of generic and family level identifications, and it is therefore not a reliable indicator in this case. The calcareous soil indicated in feature 14495 (by *Onthophagus joannae* Goljan) is further supported by the presence of the large ground beetle *Carabus violaceus* L., the lady bird *Scymnus frontalis* (F.), and to a lesser extent the ground beetle *Calathus fuscipes* (Goeze). This is not surprising for this location in Skåne due to the local geology.

Perhaps the most interesting difference between this feature and 14495 is the increased presence of *General synanthropic* species – those that are generally associated with environments strongly influenced by human actions. This habitat group overlaps to some extent with *Mould beetles*, and the taxa in this case suggest an amount of unspecified decaying material in the surroundings. Many of these species, including members of the *Enicmus* and *Corticaria* genera found in the samples, are common indoor guests and, when found in larger numbers can indicate stored foodstuffs or mouldy hay or timber. Low abundances, and generic identifications here, however, prevent further conclusions from being drawn. The Elaterid *Athous haemorrhoidalis* (F.) is entirely responsible for the *Dry dead wood* signal, which may not be entirely correct. Whilst the adults appear in woodland, the larvae live on the roots of grasses.

A general picture of a messy, inhabited dwelling site is presented by sample S10-20, and to a lesser extent by sample 0-10. Only the upper sample shows any real indication of the presence of water, and the sediments may have been deposited in a well or animal watering hole.

The various BugStats outputs for feature 26551 have useful illustrative value, in that they clearly demonstrate the need for standardizing reconstruction values to enable proper inter-sample comparisons to be made. The difference between the standardized plots is minimal – the low abundances leading to small multipliers for the taxa, which do not give any significant change in the overall shape of the diagrams. The raw diagrams also appear reasonably similar to each other, if one ignores the x-axis scales, which obviously are much larger on the abundance weighted figure. However, when one compares the raw diagrams with the standardized diagrams, a considerable difference can be seen. The extreme difference between the two samples, in terms of species richness and abundance (Table 6.12), are reflected in the raw diagrams by sample 10-20 having higher indications of environments represented. Standardization allows samples to be compared by proportioning the sample diagram components to the total sum of environmental representations for

the sample. In this case we can see that the relative extent to which some environments are represented in each sample is reversed between the figures. Evidently the high abundances in sample 10-20 bias the reconstruction.

Table 6.12. Summary counts and sums for the Lockarp 7B ‘wells’.

Feature 14495						Feature 26551	
Sample	S0-10	S10-20	S20-30	S30-40	S40-50	S0-10	S10-20
No. of taxa	5	8	15	13	4	15	40
Total abund.	5	11	26	17	5	16	63
Max abund.	1	2	4	3	2	2	4

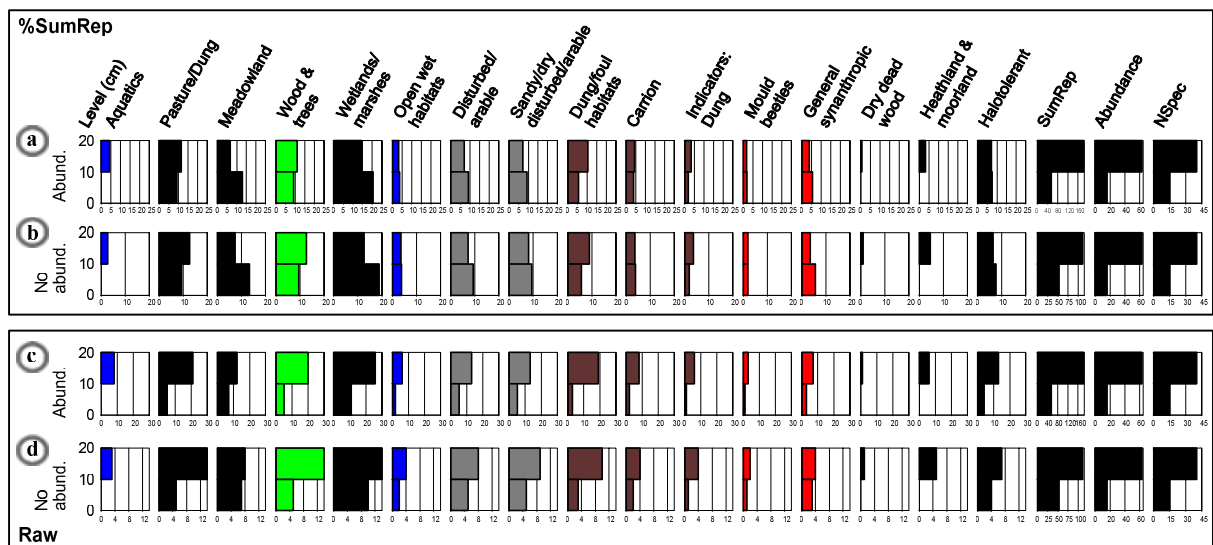


Figure 6.21. BugStats output for Lockarp 7B feature 26551, illustrating the importance of sample standardization (see text). Diagrams (a) and (a) show standardized abundance weighted and taxa only results respectively; diagrams (c) and (d) show raw counts, abundance weighted and taxa only respectively.

6.4.4 Conclusions

From the beetle evidence, Feature 14495 could very probably be a well in a settlement context, with samples 20-30 and 30-40 representing an open well in active surroundings. With such small numbers, however, it is not possible to tell whether the water would have been fit for human consumption. From the dung indications, it is most likely that animals were present in the surrounding throughout the sequence. The samples below and above this most likely represent construction and collapse phases respectively, and contain little to indicate a well or water. Although there were only a few individuals found in the latter samples, they give some indication of the catchment environment. These signals, however, are difficult to interpret due to the possibility of being secondary deposits of uncertain origin. The upper sample of Feature 26551 may represent a water trough or well in a settlement environment, with animals and decaying organic matter in close proximity.

The Lockarp results present a considerably more complex environmental picture when compared to the results from the analysis of the trap data from Koivula *et al.* (2003) (section 6.1). At Lockarp we see indications of 13 and 16 of the 22 classes in the Bugs EcoCode system, whereas the Finnish trap data indicated only 8. The most probable explanation for this is that the Koivula *et al.* data represent only one year, whereas the Lockarp samples represent an unknown, but probable multiple year span in a much more diverse environment. The longer a trap remains open, the greater the probability of rarer species being caught in it, just as the probability of surveying all species in an environment increases

with the length of survey. This relationship has been studied in detail by ecologists (Krebs, 1989), and is often seen to be log/normal – the number of new species found/trapped decreases with time. The second possible explanation is that the environment of Lockarp was indeed more complex (or patchy) than the forest-farmland transects. Urban areas/settlements provide a greater variety of microhabitats than natural or rural areas, and so will result in a greater diversity of environmental signals being given from samples.

The interpretation of fossil insect faunas requires a careful balance in the understanding of the probability of environments represented in the faunas, the nature and origin of the deposits, taphonomic processes, and ecological possibilities.

6.5 Preliminary Fossil Results from Lake Njulla, Abisko, Sweden.

6.5.1 Introduction

An attempt was made to include combined fossil insect data from the correlated contents of 14 cores from lake Njulla, near Abisko, Sweden (68°22'N, 18°42'E, 999 m a.s.l.) (Figure 6.22). The samples were provided by P     Rosen of the Climate Impacts Research Centre, Abisko. Despite the assistance of Peter Ros    , Roger Engelmark and Geoffrey Lemdahl the processing and analysis of about 500 small samples did not prove feasible^{xv} in combination with the software development which is the primary focus of the thesis. Cores were correlated optically, using digital photographs, greyscale imaging and simple manipulations to identify comparable features. All cores were taken from a small region (c. 5 m in diameter) in the area of earlier investigations (Barnekow, 1999a; Kullman, 1999; Ros    , *pers. comm.*). Magnetic susceptibility (MS) measurements were taken along cores 8 and 11 which backed up the visual correlation, although the accuracy of MS to correlate the cores was deemed insufficient for it to be used as the primary method.

The intention was to obtain beetle data to complement the existing proxy analyses from the same site (e.g. Barnekow, 1999a; Bigler *et al.*, 2003; Ros     *et al.*, 2001), and compare the temperature and environment reconstructions. Particular attention would be paid to the presence of early indications of trees, early Holocene megafossils of which (*Pinus*, *Betula* and *Alnus*) have been found at the site by Kullman (1999). Analysis of the cores is still underway, and although species numbers are too low in the individual cores to permit detailed analyses, the correlation will allow the results to be bulked up between cores.

^{xv} Even at the rapid rate of half a day per sample, this would take 250 days.

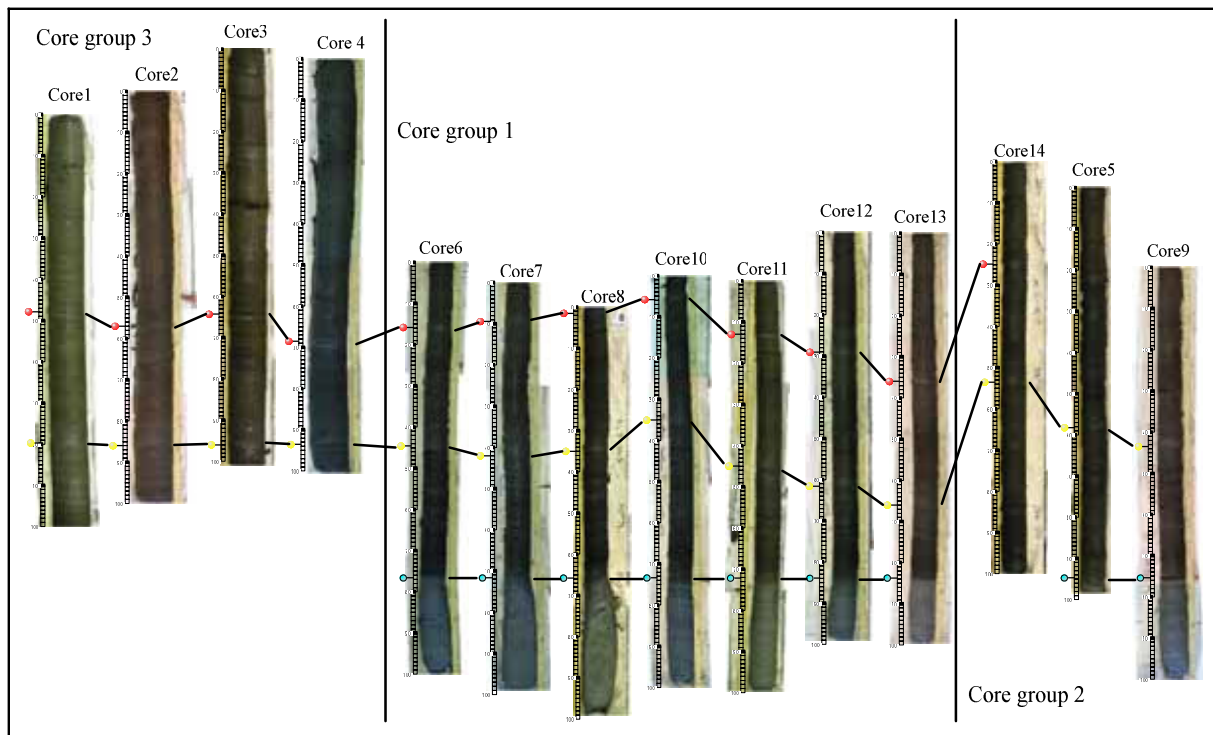


Figure 6.22. Correlation of cores from Lake Njulla, Abisko, Sweden. Lines indicate correlation horizons between the cores. Core group 3 was taken with a larger corer bore and was not able to penetrate as deep as the others. Core group 1 is considered as the most reliable set of cores.

6.5.2 Preliminary results

Partial results are available from cores 6 and 8^{xvi}, although no attempt has yet been made to bulk up the numbers of individuals by core correlation. Approximate ages have been derived by comparison of the gyttja-clay boundary found in Njulla lake samples by Barnekow (1999b) and Bigler *et al.* (2003), and suggest that analysed material dates from between 3 880 ¹⁴C BP and 8 200 ¹⁴C BP. The present day (1960-1990) mean July temperature of the area is c. 8.1°C Barnekow (1999b), and the preliminary reconstruction shows the majority of Early-mid Holocene temperatures to have been at least, and probably more than, 1°C warmer.

The gyttja-clay interface, dated to 8 200 ¹⁴C BP by Barnekow (1999b), of Core 8 appears to suggest a slightly colder winter temperature, when compared to the samples from the levels above, as indicated by the cold tolerant *Pycnoglypta lurida* (Gyll.). This species is known from a number of Lateglacial and mid-Devensian sites in the UK (see the BugsCEP records for a list of sites). There may be a slight indication of an Early Holocene, between c. 6 960 ¹⁴C BP and c. 8 200 ¹⁴C BP, warmer than the rest of the sequence, although the data are too sparse for any distinct conclusions to be drawn. Core 6 displays a similar Early Holocene thermal picture to Core 8. There are also important climatic indicator species present, such as the continental, cold tolerant, *Mannerheimia arctica* (Er.), which have no reference data in the current MCR dataset.

The preliminary habitat reconstruction results suggest a heathland environment, with more or less continuous indications of water nearby, as would be expected for samples from high altitude lake deposits. Interestingly, the only indications of woodland and trees occur during the aforementioned potentially warmer period, which supports the macrofossil evidence of Barnekow (1999b) and potentially Kullman (1999), although indicators of specific tree species have yet to be found. The evidence, however is only from three individuals of the genus *Quedius*, which are predatory and able to utilise under a broad range of habitats, and should be regarded as tenuous until more specimens are

^{xvi} Processed by Philip Buckland and Peter Rosén, and identified by Geoffrey Lemdahl.

identified. There are also potential dung indicators, such as *Tachinus laticollis* Grav. and *T. rufipes* (L.) present during this period, although these particular species are quite eurytopic. The only indication of running water is to be found at the gyttja-clay interface, in the form of *Elmis aenea* (P. Müller), and the lack of such species in later deposits could potentially be an indication of the absence of flowing glacial melt-water which was present at the start of the sequence.

6.5.3 Conclusions

Bigler *et al.* (2003) showed that although July temperature reconstructions from pollen, diatoms and chironomids for lake Njulla provided consistent patterns for the last 6 000 years, the Early Holocene evidence was variable. Although individuals have been identified from only a few samples, the beetle evidence shows much potential for providing a terrestrial proxy for early Holocene climate change in the Abisko region, and thus complementing the existing interpretations. In addition, the potential of Coleoptera to indicate the presence of vegetation types difficult to identify in the pollen and plant macro records may help provide a more detailed picture of the evolution of the landscape surrounding the lake.

6.6 Modern Case Study: Pitfall Trap Data from the area of Gården under Sandet (GUS), Greenland.

Primary references: Buckland *et al.* (1998); Buckland (2000)

6.6.1 Aims and introduction

This small modern fauna was examined by this author in Buckland (2000) and with others in Buckland *et al.* (1998). It is briefly examined here to see how the application of Bugs EcoCodes affects the interpretation, and to test the investigative power of BugStats on a low diversity, low species richness modern species list. A comparison is made with principle component analysis (PCA) of the same fauna for illustration.

During the summer of 1995 a pitfall trapping and search exercise was conducted, by the author of this thesis, during the period of excavation of the Norse Farm site Gården under Sandet (GUS) in the area of the former Western Settlement of Norse Greenland (Buckland *et al.*, 1998). Vegetation zones were described onsite by Julie Ross (*pers. comm.*), and are summarised in Table 6.13. Information on the trapping setup and other results can be found in Buckland (2000).

Table 6.13. GUS modern, vegetation zone field descriptions.

Zone	Description
A	Upper floodplain, very low birch and sedges
B	Dwarf birch-rhododendron scrub (<i>Betula</i> - <i>Rhododendron</i>)
C	Bog – moss and coarse grasses
D	Willow dominated woodland with Labrador Tea under growth (<i>Salix</i> - <i>Ledum</i>)
E	Pondside marshland, sedge and moss dominated
F	Exposed hillside grassland

6.6.2 Results

The short species list is presented in Table 6.14. The zone sums are the total Coleoptera catches for all eight traps in a zone over a four week period from mid June to mid July.

Table 6.14. GUS modern species list, zone abundance sums for the four week collection period.

Species Name	Asum	Bsum	Csum	Dsum	Esum	Fsum
<i>Patrobis septentrionis</i> Dej.	0	0	1	0	0	0
<i>Hydroporus morio</i> Aubé	0	0	0	0	1	0
<i>Colymbetes dolabratus</i> (Payk.)	0	0	0	0	4	0
<i>Gyrinus opacus</i> Sahl.	0	0	0	0	1	0
<i>Mycetoporus nigrans</i> Maekl.	1	3	1	0	6	0
<i>Simplocaria metallica</i> (Strm.)	0	2	0	0	1	0
<i>Simplocaria elongata</i> Sahl.	0	1	0	0	0	0
<i>Byrrhus fasciatus</i> (Forst.)	2	2	1	0	0	1
<i>Nephus redtenbacheri</i> (Muls.)	0	0	0	0	0	2
<i>Coccinella transversoguttata</i> Fald.	4	1	0	1	0	0
<i>Otiorhynchus arcticus</i> (O. Fabricius)	1	1	1	1	0	1

6.6.3 Discussion

The zone sum data were imported into BugStats, and two output options chosen for presentation: non-weighted percentage, and abundance weighted raw, to illustrate the problem of interpreting small faunas. Figure 6.23 shows the results of the summed trapping and hunting data for each zone (A-F). What is immediately apparent is that Zone E, the pondside, is clearly visible by the graphs of aquatics and standing water indicators. The bog, Zone C, is also visible in terms of a wetland/marshland indication, but to a lesser extent. The other zones are not so easily identified from the graphs. The upper floodplain (A), dwarf scrub (B) and grassy hillside (F) show almost identical results, although the importance of abundance is clearly shown on the raw data diagram. This may indicate that these habitats are within the scope of variation for open, grassy landscapes in Greenland, or that the system is not sensitive enough to identify these environments with such small numbers of individuals. The two individuals found in Zone D, the (dwarf) willow woodland, vaguely indicate *Meadowland* and *Heathland & moorland*, but give no forest indication, being eurytopic, rather than woodland species.

These results suggest that low diversity/abundance data are, unsurprisingly, not ideal for environmental reconstruction. This indicates that the interpretation of small fossil assemblages should be undertaken with equal care, and that a qualitative indicator approach is likely to be more productive than semi-quantitative or statistical reconstruction. However, the fact that the bog and pond were correctly identified does prove that even small datasets may have some use, even if it is very biased towards very general habitat groups such as the aquatics.

As a comparison, the first two PCA components of the same data were examined with respect to species and samples (Figure 6.24 and Figure 6.25). Although PCA is not recommended for such small datasets, it is used here to illustrate the potential of BugStats for extracting information from these. BugStats failed to clearly illustrate more than the pondside and bog zones, and the PCA results are not particularly informative.

From Figure 6.25 we can see that Zone E (pondside) differentiates itself from the other zones on the first component axis. This could be explained in terms of the aquatic nature of the sample fauna, although the hypothesis of the first component representing a hydrological gradient is weakened by the position of Zone C (bog), the (qualitatively) next wettest site, at the middle of the spread of data. This could either be explained in terms of the particularly dry year, or in terms of the representativeness of the small fauna. On the second component axis of the species diagram (Figure 6.24) one can see the effect of the relative high abundance of *Mycetoporus nigrans*, a small rove beetle inhabiting moss and humus layers, which was new to Greenland with this work. Although the species is stenotopic to these environments, these themselves are quite widespread around the GUS site.

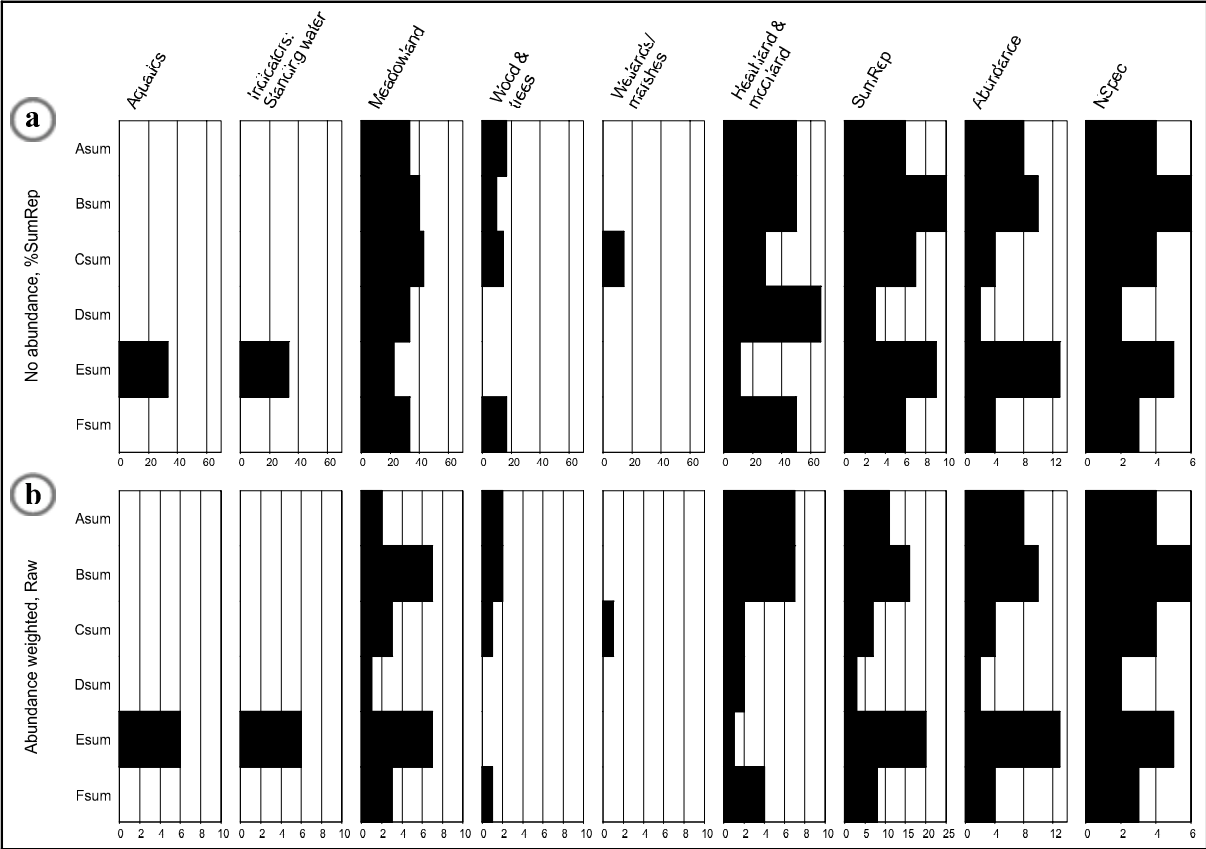


Figure 6.23. BugStats output for GUS modern data, showing (a) standardized, taxa only reconstruction, and (b) abundance weighted, raw counts based reconstruction.

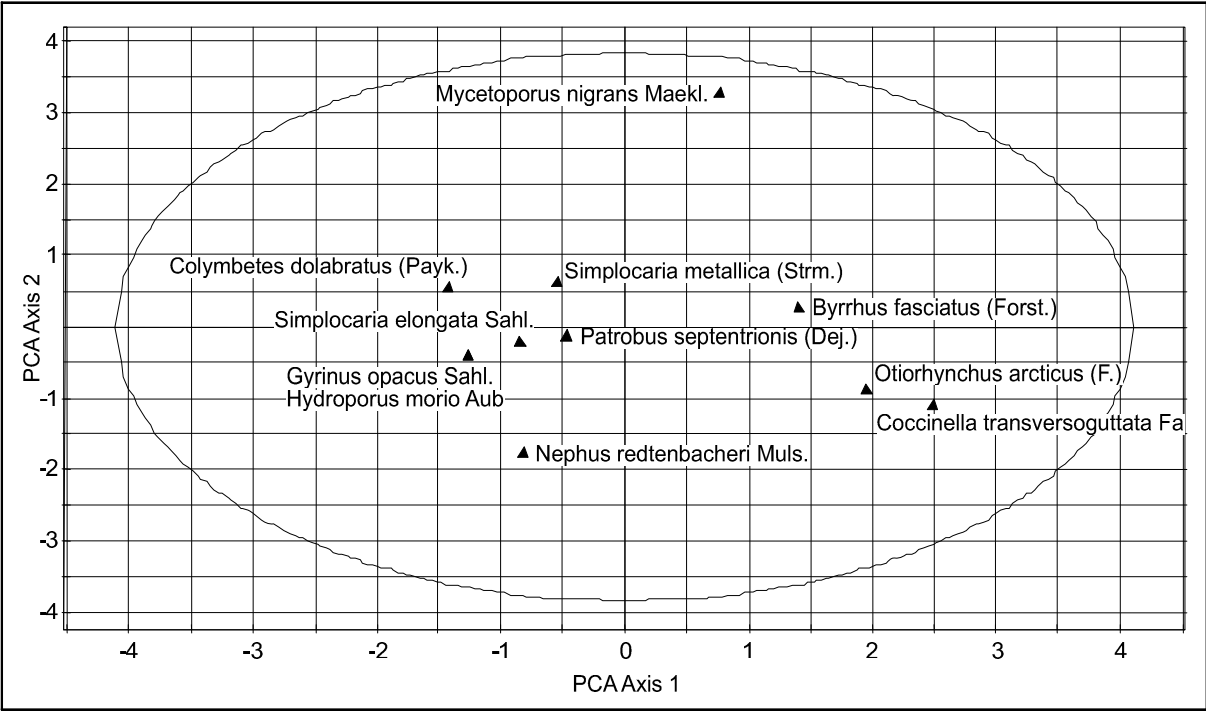


Figure 6.24. First two components of PCA on the GUS modern pitfall trap data, showing species names.

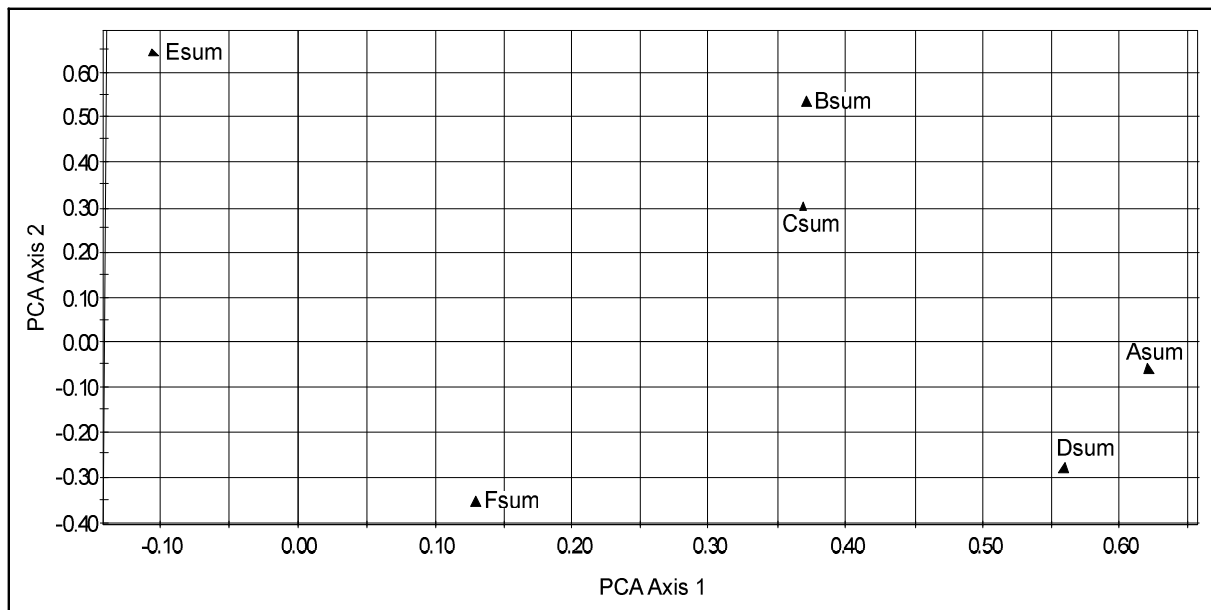


Figure 6.25. First two components of PCA on the GUS modern pitfall trap data, showing vegetation/sampling zones.

6.6.4 Conclusions

If one were to consider the fauna above as a fossil assemblage, one would be hard pressed to identify correctly more than the wetter zones E and possibly C. The presence of a number of water beetles in the former is enough indication of the presence of water close by. The relative dampness of the bog Zone C could be established from the examination of the fauna, but is not easily seen from the PCA. Neither the PCA grouping of Zones B and C, nor A and D, is easily explained in terms of the local environment. There is a risk that further attempts to explain such low abundance and diversity sites would lead to over-interpretation. In conclusion, without prior knowledge of the environment at the time of deposition, PCA is of little use on this type of small fauna. BugStats on the other hand was able to identify specific habitat components, due to its use of internal habitat reference data for each taxon. It may therefore be a more useful tool when undertaking habitat reconstruction from Quaternary deposit than ordination techniques.

6.7 Fossil Case Study: Climate and Environmental Change in Europe over the Past 20 000 ^{14}C years Reconstructed from Coleopteran Remains

Data source: BugsCEP

6.7.1 Aims

The aim was to reconstruct a general picture of the thermal regime of Europe for the last 20 000 years, in 1 000 year time slices, using the data available from ^{14}C dated samples in BugsCEP. By grouping together samples from a wide geographical area, into broad time slices, it may be possible to simulate the type of assemblages that would be expected where samples from a single site encompass environments or climates that change faster than the resolution of the samples. It should then be possible to evaluate the ability of the jackknife method to identify such assemblages, and thus provide indications of the reliability of a particular temperature reconstruction. The reconstruction is compared with existing published reconstructions, and the reliability of the former discussed, with respect to thermal gradients and the representativeness of the time slice assemblages. A habitat based

reconstruction is presented for the same data, in the interest of identifying general trend in the evolution of European environments.

6.7.2 Introduction

A number of biological proxy derived reconstructions of the past 10-20 thousand years of European climate have been undertaken (e.g. Davis *et al.*, 2003) at a variety of resolutions, and overviews can be found in a number of general texts (e.g. Battarbee, 2004; Bell & Walker, 2005). Similar reconstructions from Coleoptera have been undertaken by Coope & Lemdahl (1995), Coope *et al.* (1998) and others. The aim here is to see how a general European millennial scale climate reconstruction using the sites in BugsCEP and the BugsMCR utility is similar to earlier reconstructions. BugStats is also used to produce a general environmental reconstruction for the same period and area, and the implications of this discussed in relation to the variability in the thermal reconstructions. In addition, a correlation coefficient is used to assess the similarity of faunas between time slices. For a more detailed description of the mechanics of the reconstructions see chapters 4 (BugStats) and 5 (BugsMCR). All dates are given in ^{14}C years.

A naive approach to the dating of sites is used here, with no age depth curves being constructed and only samples with direct ^{14}C dates being used. No attempt is made to assess the differential reliability of the dates, and it is possible that a number of bulk dates are included. The broad nature of the time slices may help to minimise the effects of these. The implications of individual sites for reconstruction will not be discussed in detail, and this section should be considered more of an experiment than an absolute description of the past 20 000 years of climate and environmental change.

6.7.3 Sites

Queries were created within BugsCEP to limit the sites extracted to those within European countries, with Greenland excluded due to its distance from mainland Europe and the potential for the Greenland icecap and Atlantic Ocean making any temperature reconstructions significantly different from those of mainland Europe. The position of the Fennoscandian ice sheet will also have had a significant impact on the climate of various time slices (Coope *et al.*, 1998), and due to the geographical range of sites used this impact will vary. Figure 6.26 shows the geographical distribution of 77 sites included in the reconstruction, and Table 6.15 the site names, and time slices that they represent. This is coincidentally the same number of sites as used by Coope *et al.* (1998) to investigate temperature gradients in northern Europe, although the list of sites is not identical, with only 28 sites being common to the two reconstructions. A further 23 sites are present in BugsCEP but either their species lists or dating evidence have yet to be entered fully, and the model will be updated in the near future^{xvii}. The use of age-depth curves for partially dated sites could have increased the size of the dataset considerably, but would have required closer examination of the individual sites and lies beyond the scope of this thesis. The author is reluctant to apply a generic linear age-depth curve to all sites due to the potentially variable nature of the sediments sampled, and the lack of sample depths for a number of important sites in BugsCEP. Such an approach was undertaken by Davis *et al.* (2003) using European pollen data, with a dataset which allowed for a considerable amount of spatio-temporal interpolation. It should be noted that the dominance of sites in the British Isles will undoubtedly have influenced the reconstructions, as will the few more southerly sites (Figure 6.26 and Figure 6.27). This is, of course, not an ideal distribution of sites for a single reconstruction, but they are used here to illustrate a number of points for discussion. Although Coope *et al.* (1998) demonstrated both latitudinal and longitudinal gradients in glacial-Holocene transition temperatures, only a plot of the latitude of sites per time slice is provided here (Figure 6.27). Factors associated with latitude are controlling factors in biodiversity (Mittelbach *et al.*, 2007), and the latitudinal spread of sites may therefore affect the environmental reconstructions. It is important to remember that, due to the nature of the method, the MCR temperature reconstructions will represent the mutual range of the

^{xvii} 13 of the sites used by Coope *et al.* (1998) use unpublished data that has not yet been published or acquired for inclusion in BugsCEP.

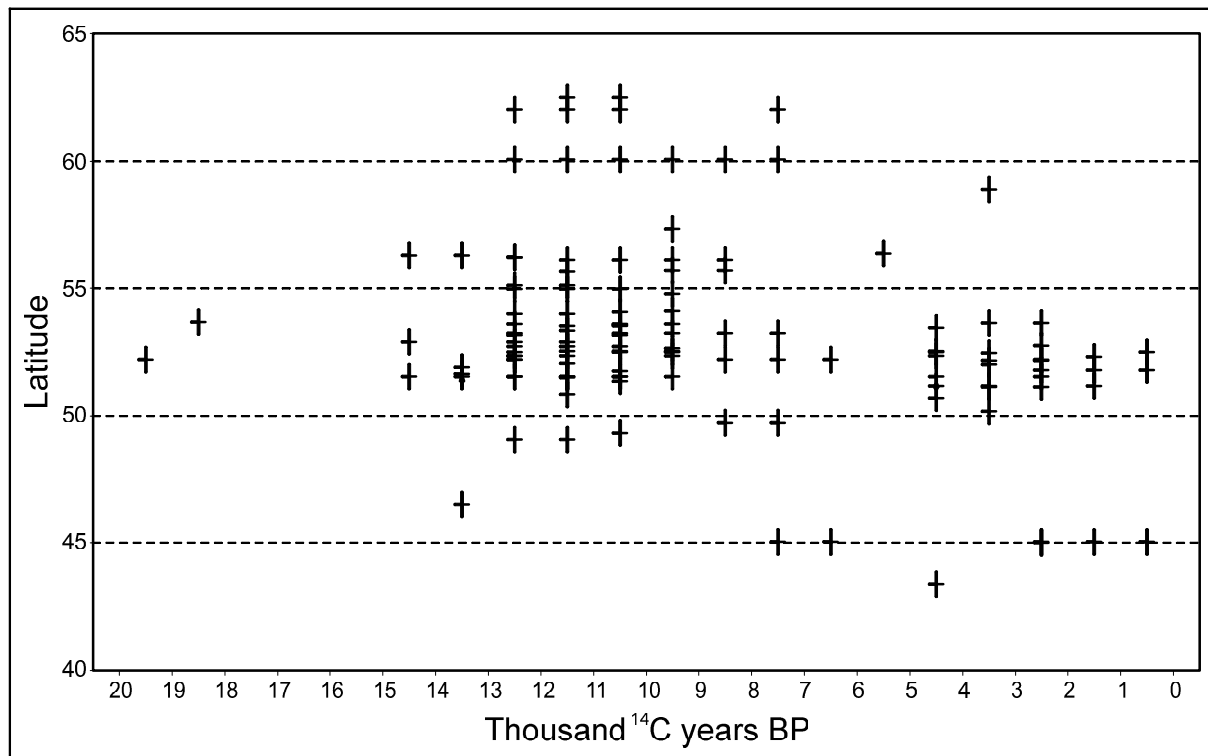


Figure 6.27. Plot of latitudes of sites in the 20 000 ¹⁴C year reconstruction, per time slice.

Table 6.15. List of sites used in the 20 000 ¹⁴C year, 1 000 year time slice reconstruction, indicating the time slices for which each site has ¹⁴C dated samples. Note the absence of time slices 18-17K, 17-16K and 16-15K which produced no data. See BugsCEP for references for all sites.

No.	Site Name	Country	19-20K	18-19K	14-15K	13-14K	12-13K	11-12K	10-11K	09-10K	08-09K	07-08K	06-07K	05-06K	04-05K	03-04K	02-03K	01-02K	00-01K
1	Okruglo	Croatia															X		
2	Abbots Way	England													X	X		X	
3	Abingdon	England				X													
4	Alcester: Alluvial	England									X	X	X						
5	Alcester: Coulter's Garage	England															X		
6	Armthorpe	England						X											
7	Aston Mill: Late Holocene	England														X			
8	Baker site	England												X					
9	Barnwell Station	England	X																
10	Baston Fen	England					X	X											
11	Bidford on Avon: Pilgrim Lock	England														X	X		
12	Colnbrook	England				X													
13	Colney Heath	England				X													
14	Croft	England							X					X					
15	Croydon	England							X										
16	Davenham: Church Moss	England					X	X	X	X	X								
17	Dimlington	England		X															
18	Farmoor: Late Glacial	England							X										
19	Gransmoor	England					X	X											
20	Isleham	England													X				
21	Lea Marston A	England						X											
22	Lea Marston B	England							X										
23	Leicester: Early Holocene	England							X										
24	Messingham	England							X										
25	Misterton Carr	England												X					

No.	Site Name	Country	19-20K	18-19K	14-15K	13-14K	12-13K	11-12K	10-11K	09-10K	08-09K	07-08K	06-07K	05-06K	04-05K	03-04K	02-03K	01-02K	00-01K
26	New Shide Bridge	England												X					
27	Northmoor LG	England					X												
28	Porth Meare Cove	England														X			
29	Ramsey Heights	England														X			
30	Red Moss	England				X		X	X										
31	Ripon	England							X										
32	Rodbaston Hall	England						X											
33	Rowlands Track	England												X					
34	Shustoke	England												X					X
35	Sproughton	England					X												
36	Stourport	England															X		
37	Thorne Moors Trackway Site	England														X	X		
38	Tiln	England					X												
39	Tinney's Brushwood	England														X	X		
40	West Bromwich	England				X		X	X										
41	West Drayton	England					X												
42	Wilden	England				X	X		X										
43	Yarborough Quarry	England						X											
44	Yarnton	England															X	X	X
45	Yoxall Bridge	England															X		
46	Conty	France				X	X	X											
47	Havre	France								X	X								
48	Houdancourt	France				X	X												
49	La Borde	France						X											
50	Skalafjordur	Faroes									X								
51	Taillefer Massif	France									X	X					X	X	X
52	Tourves	France												X					
53	Ballybetagh	Ireland				X		X											
54	Drumurcher	Ireland						X											
55	Shortalstown	Ireland				X													
56	Notsel, Mark Valley	Netherlands				X	X	X											
57	Usselo	Netherlands				X													
58	Godøy	Norway					X	X											
59	Zabinko	Poland				X													
60	Bigholm Burn	Scotland					X												
61	Brighthouse Bay	Scotland							X										
62	Clefftnadal	Scotland				X	X	X	X	X	X								
63	Heldalewater, Hoy	Scotland														X			
64	Kinfauns	Scotland											X						
65	Redkirk Point	Scotland				X	X	X											
66	Roberthill	Scotland				X													
67	Teith Valley	Scotland				X													
68	Torrie Borehole	Scotland				X													
69	Björkeröds Mosse	Sweden		X	X														
70	Bysjön	Sweden					X												
71	Hanobukten	Sweden							X	X									
72	Körslättamossen	Sweden					X	X	X	X									
73	Ranstad	Sweden							X										
74	Lausanne	Switzerland			X														
75	Glanllynau	Wales		X		X	X												
76	Llanilid	Wales		X	X	X	X	X	X										
77	Redwick	Wales												X		X			

6.7.4 Methods

The BugsCEP database was used to extract abundance data for the past 20 000 ^{14}C years, in 1 000 year time slices, using only ^{14}C dated samples from stratigraphic sequences. Only data from European sites, with the exclusion of Greenland, were used. A total of 3 768 taxon occurrences were retrieved, populating the time slices as shown in Table 6.16. The effective meaning of the cell values are explained in Table 6.17.

Although some samples have more than one ^{14}C date, only one instance of the affected taxa occurrence is included in the calculation lists, thus preventing over representation of the taxa concerned. Due to the presence/absence nature of the method, MCR reconstructions are unaffected by this, whereas the abundance weighted environmental reconstructions are extremely sensitive, and would give grossly exaggerated habitat signals for samples with more than one date.

Table 6.16. Summary of samples and species occurrences from 1 000 year time slices for the past 20 000 ^{14}C years. An 'occurrence' is a fossil record of a specific taxon in a specific sample, and may either be an abundance or presence value, see Table 6.16 for more details. Note the important difference between the number of taxa (NSpec), and the number of taxa available for MCR (No. MCR Taxa).

Time slice	No. Sites	No. Samples	Occurrences	No. Taxa (NSpec)	No. MCR Taxa	Total Abundance	MCR Abundance
00-01K	3	3	265	241	50	772	146
01-02K	4	6	376	258	65	1288	230
02-03K	9	11	923	480	95	3328	623
03-04K	8	11	527	258	54	2044	429
04-05K	10	10	435	274	62	1186	191
05-06K	1	1	4	4		4	
06-07K	2	2	66	65	10	226	35
07-08K	6	8	132	108	26	303	76
08-09K	6	10	152	107	18	264	48
09-10K	13	28	1156	385	95	5154	1327
10-11K	19	26	1302	544	136	7248	2521
11-12K	20	46	2142	428	140	6120	2478
12-13K	20	31	1387	411	140	2979	1033
13-14K	6	8	206	135	43	491	131
14-15K	3	4	48	40	15	63	25
15-16K							
16-17K							
17-18K							
18-19K	1	1	26	13	6	26	12
19-20K	1	5	27	21	9	31	14
Instance Totals			9166	3768	964	31541	9319
Unique Totals	77	186		1306	271		

Table 6.17. Explanation of cell and total values in Table 6.16.

	Time slice	Instance Totals	Unique Totals
No. Sites	Number of sites representing time slice		Number of sites in dataset
No. Samples	Number of samples representing time slice		Number of dated samples in dataset
Occurrences	Number of fossil records in time slice	Total number of fossil records	
No. Taxa (NSpec)	Number of unique taxa per time slice	Sum of time slice numbers	Number of unique taxa
No. MCR Taxa	Number of unique MCR taxa per time slice	Sum of time slice totals	Number of unique MCR taxa
Total Abundance	Total number of individuals in time slice	Total number of individuals in dataset	
MCR Abundance	Total number of MCR individuals for time slice (used in climate reconstruction)	Total number of individuals used in MCR reconstruction	

A climate reconstruction was produced for the times slices using BugsMCR (Figure 6.28). The slices were also subjected to a jackknifed MCR reconstruction in order to see the effect of removing one species at a time on the reconstructed temperatures. This could provide information on the internal reliability of each MCR reconstruction by highlighting the degree of variation in the samples. Additional counts and statistics, which are not standard BugsMCR outputs, are provided with each temperature diagram to support the discussions.

The modified Sørensen correlation coefficient (Southwood, 1978) was calculated to provide an indication of the faunal similarity between slices (Table 6.18). This was run using all taxa, and the method is abundance sensitive, which may have the effect of enhancing the difference between low and high abundance slices. The comparison with independent faunal groupings earlier in this chapter (section 6.2.5) suggests, however, that the resultant groupings are viable when compared to those delimited on the basis of ecological knowledge.

A Bugs EcoCode based environmental reconstruction was performed using a variety of settings. Only standardized, as a percentage of the sum of representations (%SumRep), diagrams are presented, as the high variation in species numbers and abundance values between samples rendered the other diagrams practically useless for the comparison of habitat indications between time slices. Calculations were performed using both ‘all taxa’ and ‘species level identifications only’ settings, in order to identify variations in the effect of higher level identifications on the reconstructions. It is possible that generic level identifications are proportionally more common in samples from colder or more disturbed periods, and that their removal will reduce the environmental resolution of these samples. See Chapter 4 for a full explanation of the reconstruction settings and their implications.

6.7.5 Results and discussion

As explained in Chapter 5, BugsMCR does not employ the calibration/correction method of Atkinson *et al.* (1986), and outputs a range of temperatures in which all values are equally probable on the basis of the assemblage underpinning the reconstruction. These ranges present a more realistic reconstruction of large time slices than a corrected single value, due to the fact that temperatures will have undoubtedly varied during the time slice, and that the single value cannot express this. As yet, the correction method is not able to provide sample based error estimates, and so standard deviations are not available to simulate the range of values derived from a raw MCR calculation. Despite this, the corrected values of previous authors (e.g. Coope *et al.*, 1998) should fall within the range of uncorrected MCR values, and thus be comparable to an extent. A number of other authors have presented both corrected and uncorrected data, which makes comparison easier. Although there are a

number of interesting differences between the reconstruction presented here and a number of previously published temperature curves, the majority of time slices coincide with the ranges of previous publications. The regional comparison presented by Coope & Lemdahl (1995), which illustrated local variations in Lateglacial-early Holocene climate change, may help in explaining some of the differences between the general reconstruction and specific regional curves.

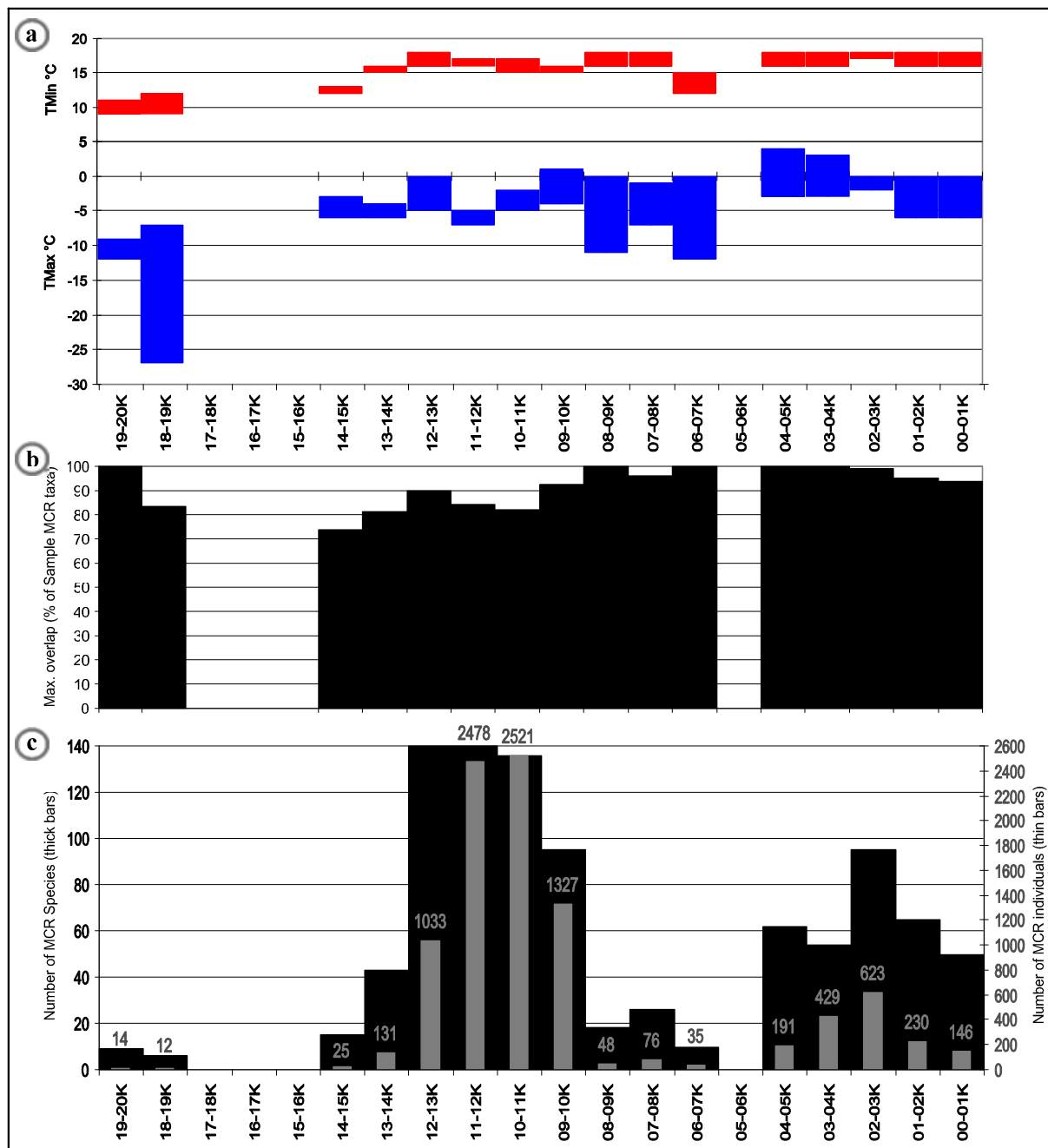


Figure 6.28. MCR temperature reconstruction for the last 20 000 ^{14}C in 1 000 year slices using all European ^{14}C dated stratigraphic sequence samples in BugsCEP (Greenland excluded). (a) Bars represent the possible range of temperatures as indicated by the beetle faunas, for TMax and TMin; (b) the percentage of species in the area of maximum overlap from which the MCR values are calculated; (c) number of taxa (thick black bars), and individuals (thin grey bars) used in the reconstruction.

Despite the large number of species involved (up to 140 in time slices 12-13K and 11-12K), at least 75 % of species represented the area of greatest overlap in each of the time slices that included MCR taxa (Figure 6.28b). This suggests that, despite the large geographical spread of sites, the majority of

the faunas represented are relatively thermally homogenous. Although the time slices are large, and arbitrary in terms of their boundaries, a degree of comparability is displayed between Figure 6.28a and earlier reconstructions, although it differs between TMax and TMin.

Glacial-early Holocene transition

Whilst TMax shows a progressive rise in summer temperature values from 12-13°C to 16-18°C between 15 ka and 13 ka BP, TMin does not. The Lateglacial-early Holocene TMax reconstruction is in reasonable agreement with the British Isle reconstructions of Atkinson *et al.* (1987) and Coope & Lemdahl (1995), although the range of temperatures reconstructed for 13-14K are towards the upper limits of what would be expected. TMin, on the other hand, fails to resolve the expected lower temperatures of the 14-15K time slices. It also indicates a significant dip in winter temperatures between 12 ka - 11 ka BP, followed by a rise to the warmest winter temperatures reconstructed for the Early Holocene (09-10K), a pattern which is not mirrored by TMax. It would appear that the thermal range of the sites used disguises the Younger Dryas as identified in the British fossil beetle record to 11-10 ka BP (Atkinson *et al.*, 1997), or for some reason makes it apparent in the earlier time slice. It may be possible to explain this in terms of the presence of Scandinavian sites in these sample, which, probably due to the close proximity of the Fennoscandian ice sheet, do not synchronously show the same climate development as the British Isles for the period 13 ka to 9 ka BP (Coope & Lemdahl, 1995). The Bølling/Allerød Interstadial, c. 13-11 ka BP (Bell & Walker, 2005), is well reconstructed with the warmer 12-13K and colder 11-12K time slices corresponding to the Bølling and Allerød respectively. Jackknifing (Figure 6.29a) adds little to the interpretation of these slices, the reconstruction being apparently quite consistent through the sites when compared to earlier slices. It could also be that the geographical range of the sites, and thus variations in the chronology and magnitude of climatic shifts is too great to be identified by the removal of any single species. The multiple removals variation of the method (see Chapter 5) may prove more useful in such cases.

Examination of the jackknife data does, however, shed light upon the overall development of European winter temperatures during the period 15 ka-12 ka BP, and enhances the potential of the TMin values to illustrate the trend seen for TMax. Closer examination of the 14-15K time slice may help to explain the results. The individual removal of four of the species from the reconstruction result in significant downward expansion of the lower limit of TMin, although at first glance it is surprising that two of these particular species lead to the possibility of a colder reconstruction. *Boreaphilus henningianus* Sahl. and *Bembidion fellmanni* (Mann.) are both cold, stenothermic species according to their MCR data, both with TMax tolerances of 6-13°C, and so one would logically assume that their removal from calculations would allow other, less cold tolerant species to draw the reconstructed temperatures upwards, as is the case with the TMax values. The exclusion of the warm, eurythermic species *Hygrotus inaequalis* (F.) and *Chaetarthria seminulum* (Hbst.) results, as would predicted on this premise, in the downward extension of the reconstructed temperatures. Closer examination of the climate space map for the time slice shows a complex set of overlays (Figure 6.30), and suggests that at least two conflicting faunal components are involved, and from Table 6.15 we could suppose that this may be the result of the geographical location of the sites. Of the three sites, Glanllynau and Llanilid in Wales may represent a relatively warmer, more oceanic climate, whereas Björkeröds Mosse, in Sweden, may be responsible for the colder climate strongly influenced by the Fennoscandian icesheet. However, Coope *et al.* (1998) detected no such west-east gradient at this time, and the situation is not so simple. In fact, for the 14-15K time slice, none of the above mentioned species occur at Björkeröds Mosse, all of them occur at Glanllynau, and all with the exception of *B. fellmanni* occur at Llanilid. From examination of the MCR reconstructions for each site it can be suggest that the dating evidence for Llanilid, a humic substances date, may be unreliable, as the sample gives a TMax reconstruction of 17-21°C. Björkeröds Mosse is represented by only two species, *Amara alpina* (Payk.) and *Agabus bipustulatus* (L.), and five individuals in this time slice. Clearly, further well dated sites are needed for a detailed analysis.

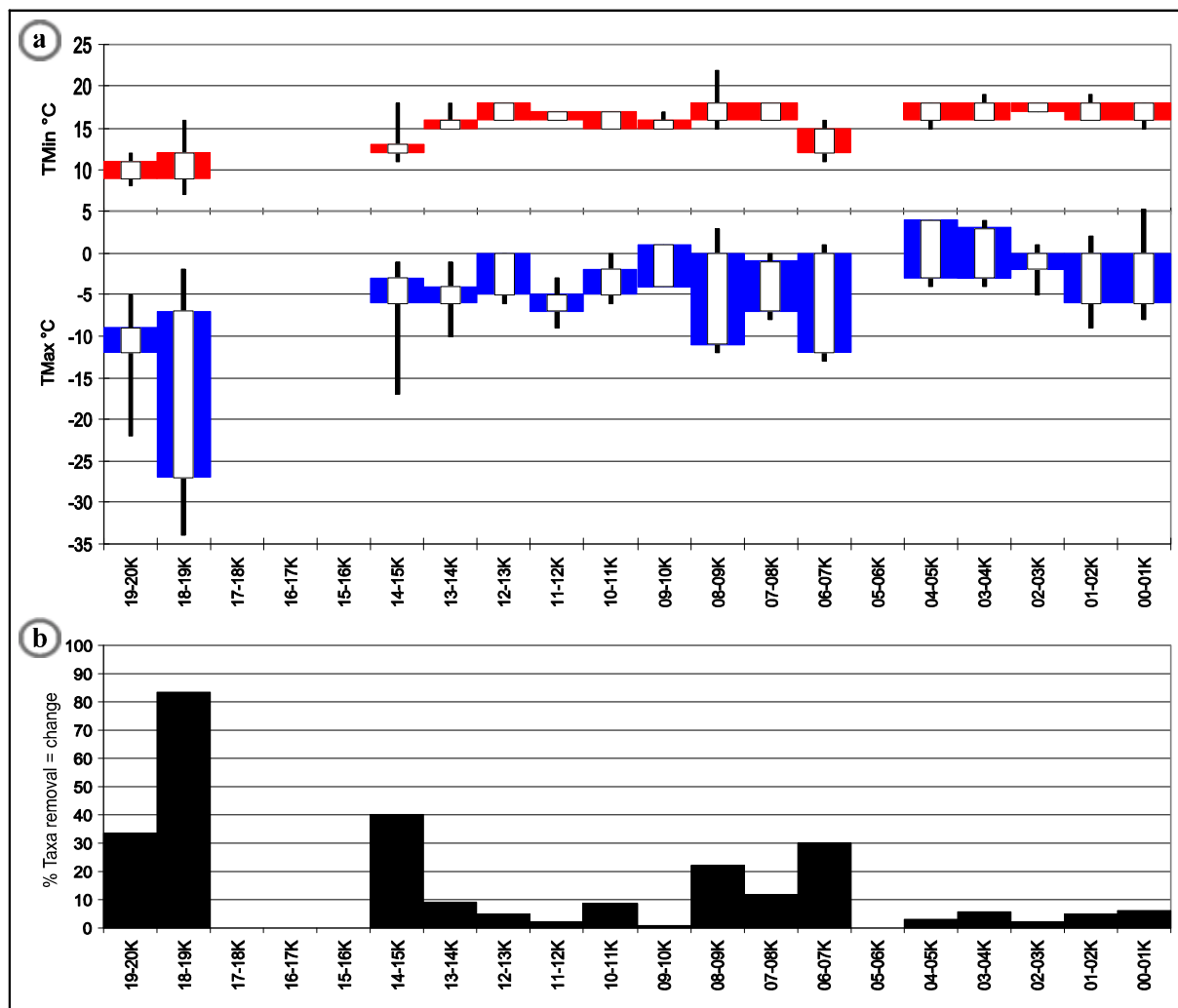


Figure 6.29. Jackknife results from 20ka temperature reconstruction, showing (a) the maximum (black extension bars) enlargement, and reduction (white boxes) of combined envelopes caused by the removal of any one taxa. The standard MCR values are shown as in Figure 6.28a. (b) shows the percentage of taxa whose removal causes a change in the reconstructed temperature range.

Both TMax and TMin realistically identify the significantly colder 20 ka – 18 ka period, with results comparable to other reconstructions of 9-12°C summer temperatures. The two millennia are represented by single sites in the British Isles, and include assemblages which represent temperatures of between 5-9°C lower than the reconstructed summer temperature for the last 1 000 years. Ideally, more data should be included in these time slices to provide a more robust reconstruction.

Fixed 1 000 year slices, rather than slices clustered by thermal characteristics, or individual sample by sample reconstructions (e.g. Atkinson *et al.*, 1987; Coope & Lemdahl, 1995), increase the probability that periods of rapid climate change will be missed in the reconstructions. Even though the 12-13K to 11-12K, and 10-11K slices could, on the basis of our current understanding of Lateglacial-early Holocene climate change, have coincided with the Bølling/Allerød and Younger Dryas periods respectively, little evidence was found for them in this reconstruction other than a slight indication in TMax values (Figure 6.28a). The changes in the percentage of species representing the area of maximum overlap (Figure 6.28b) may provide a proxy for the degree of climate change in a time slice, in that slices that encompass greater change are more likely to contain assemblages representing more thermally diverse faunas. Another possibility is that some of the variation is caused by changes in geographical thermal gradients over time, as described by Coope *et al.* (1998), or lags in climate change across Europe.

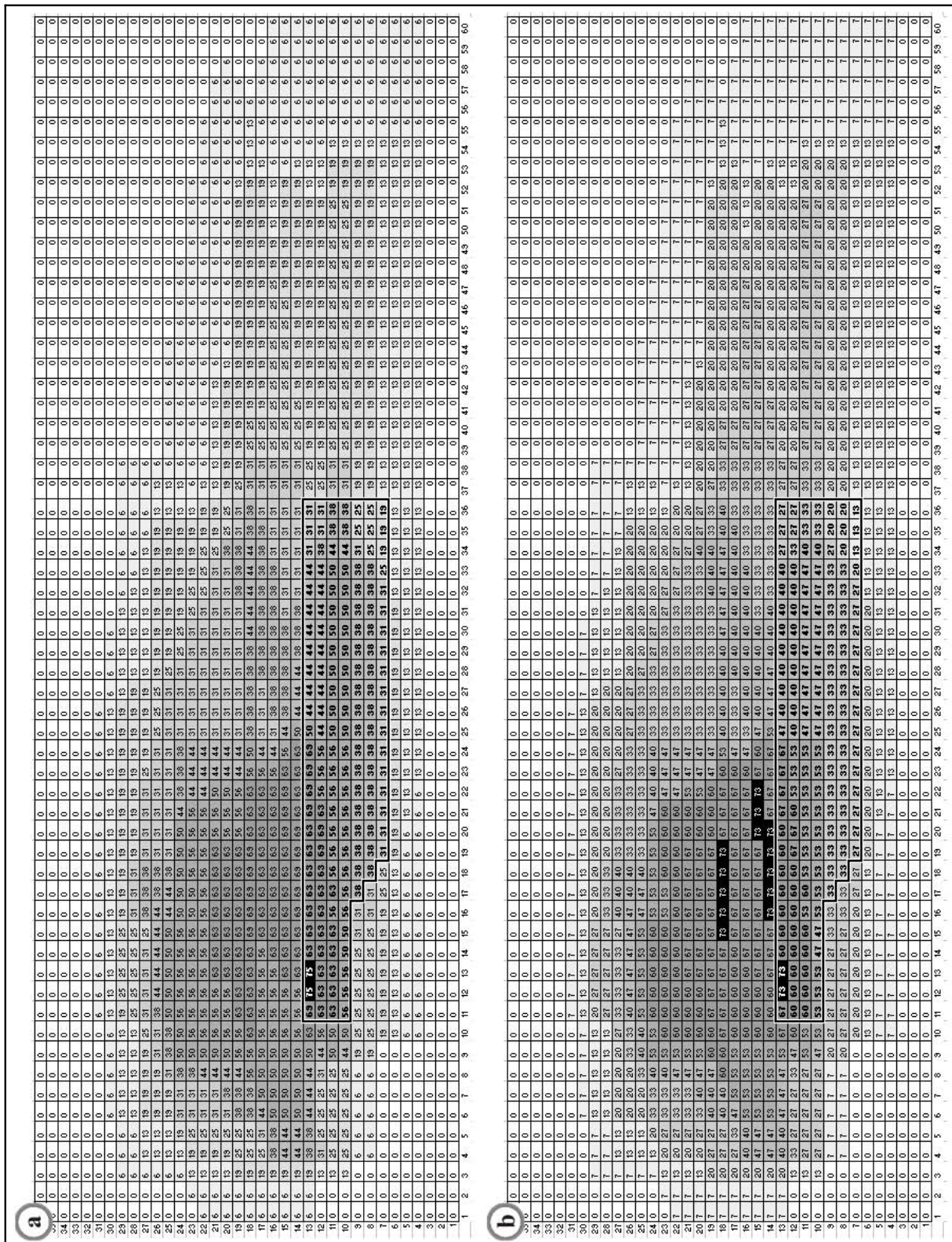


Figure 6.30. Climate space maps for time slice 14-15K, showing percentage overlaps for (a) all taxa, and (b) with *Boreaphilus henningianus* Sahl. excluded, the thermal envelope of which is outlined and shown in bold. The cells with maximum overlap, which make up the mutual climatic range are shown with white text on black cells. Note how the removal of *B. henningianus* creates a discontinuous area of maximum overlap, the outer limits of which give the MCR temperature values. This illustrates a potentially split fauna.

Early-mid-Holocene

The time slices from 8 ka to 5 ka contain considerably less data than their neighbouring time slices (Figure 6.28c), which results in less constrained T_{Min} values, suggesting a probability of colder winters. This seems unlikely on the basis of earlier reconstructions, and is most likely an artefact of the small dataset. Comparison with time slices 19-20K and 18-19K, which are based on even less data, illustrate the ability of MCR to give acceptable temperature reconstructions with even small numbers of species, although the lack of error estimation is a problem. The dating evidence for the single site in time slice 6-7K, 'Alcester: Alluvial' (Shotton *et al.*, 1977), is unreliable and the sample should most probably be moved into the 8-9K time slice. The lack of dated samples in the Early to mid-Holocene is clearly a problem. Interpolation of dates, by the application of age-depth curves would help increase the size of the dataset, but introduces another set of errors which could make the results less reliable. In this respect, BugsCEP can be used to identify areas in need of further research, and this is clearly one of them.

The jackknife results (Figure 6.29a) suggest that the reconstruction of the 8-9K time slice could be made warmer by the removal of *Patrobis assimilis* Chaud., a curytopic carabid whose thermal envelope suggests a slightly eurythermal, but cold tolerance. The majority of other species in the time slice are either warm stenotherms or eurytherms, and suggest a wider extension of the MCR into warmer climates. *P. assimilis* is found at two of the six sites representing this time slice, Clettnadal on Shetland and Hanobukten in Sweden, but only represented by one individual at each site. Obviously its presence cannot simply be dismissed on the grounds that it does not fit the pattern of the other species, just as a radiocarbon date must be explained rather than dismissed. It is possible that the species is present at one extreme of its tolerance range, or that it is a casual occurrence at both sites. In either case, its effect on the temperature reconstruction cannot easily be dismissed without treating species with equally low abundances in other time slices in the same way. The implications of filtering out low abundance species are not simple, and there is a risk of losing information, especially from low frequency indicator species.

Mid-late Holocene

The MCR reconstruction from 5 ka BP to present appears to present a consistent picture of a stable late Holocene climate. The data do suggest a swing in the variability of winter temperatures, from warmer between 5 ka and 3 ka, and colder from 2 ka to the present day, although it should be remembered that there are no modern samples in the dataset. The 00-01K time slice is poorly represented, by only three sites, and may not present a particularly reliable picture of this segment when compared to the more data rich ones. The addition of modern reference sites, and even a higher resolution beetle based MCR analysis of the past millennium, would be a worth while exercise.

Relationships within the data

The compilation of large datasets provides opportunities to investigate commonly cited statistical relationships in populations, and their applicability to fossil assemblages, as well as relationships between the output data from BugsMCR. It was stated earlier (Chapter 5) that the percentage of species whose removal leads to a change in temperature values, as a result of the jackknife method, could be a valuable indicator of reliability in reconstructions, possibly in the form of a measure of the amount of variability in an assemblage. It is commonly accepted that the number of species used in a reconstruction is a controlling factor on the reliability of any reconstruction – the more species, the greater the evidence. An approximate log-log relationship is seen between these two variables in the 20 ka dataset Figure 6.31a, suggesting that the 'percent of species removals leading to changed temperatures' variable (PctSppTDiff) may not contribute anything beyond the 'number of species' variable (NSpec). The data points become more dispersed towards the higher number of species, and the relationship needs investigating more thoroughly with site datasets, rather than using compiled pseudo-samples such as the above time slices.

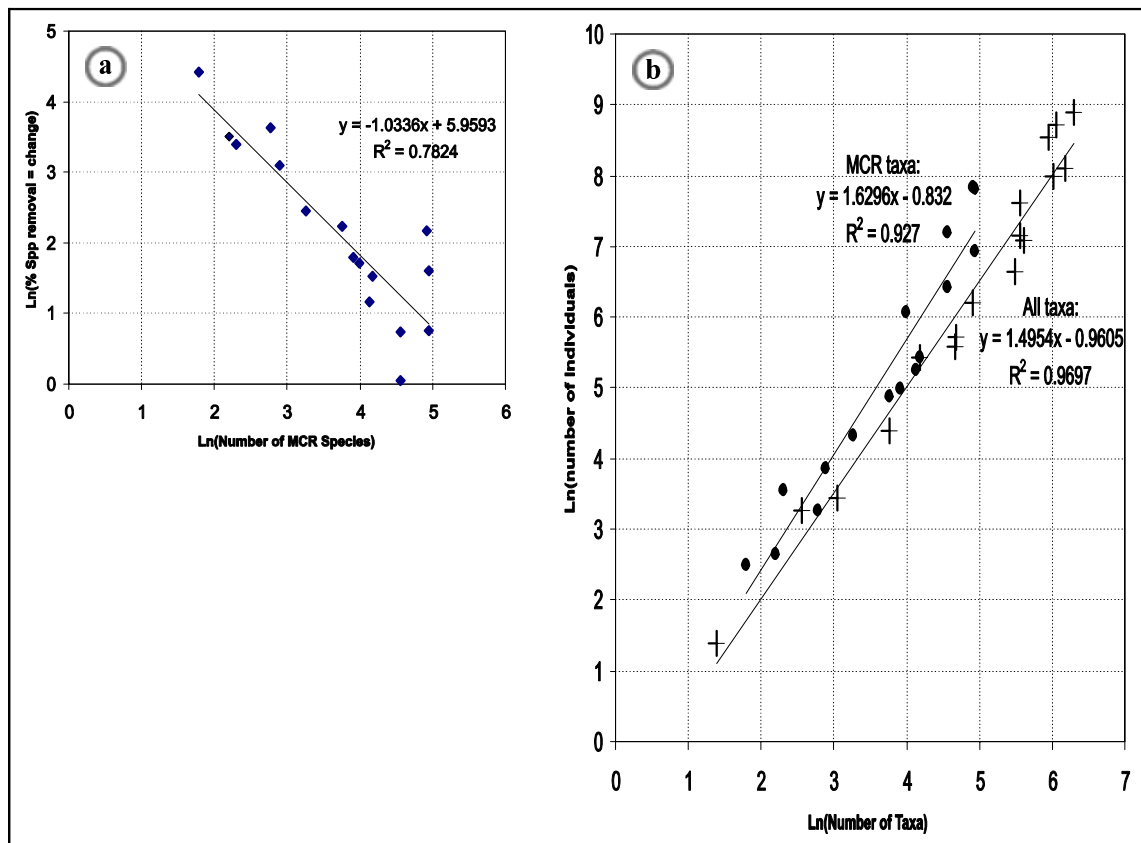


Figure 6.31. Graphs showing relationships, in the 20 ka dataset, between (a) the number of MCR species and the percentage of species whose removal leads to a change in temperature values; and (b) the number of taxa and number of individuals for the MCR subset and full dataset.

The relationship between the number of species and the number of individuals in animal populations (the S:N ratio) has been the subject of attention for many years, and a number of descriptive models exist (Southwood & Henderson, 2000). The implications of these relationships for environmental reconstruction from fossils were briefly discussed in Chapter 4. In the 20ka dataset, both the MCR species and full dataset exhibit ln-ln relationships between number of taxa and individuals (Figure 6.31b). Due to the nature of the data selection, this is in fact the relationship between the sum of (^{14}C dated) samples in each time slice, and may not represent a true S:N ratio for the individual samples. The fact that the relationship for the MCR taxa is extremely similar to that for all taxa, suggests that the subsetting of a species list to only MCR taxa does not introduce bias by changing the S:N relationship. The BugsCEP database provides an excellent opportunity to study these relationships for fossil assemblages, and more work should be done on this.

Time slice correlations

From Table 6.18 it can be seen that there are two, or possibly three clusters of similar time slices according to the modified Sørensen coefficient (see Chapter 4 and Southwood, 1978). Slices 2-3K and 3-4K are most similar, which suggests that the period 4 ka to 2 ka BP was faunally, and thus environmentally, relatively stable. Only two of the 14 sites representing this time period are outside of the British Isles, however, so the pattern may only be valid for this small area of Europe. It is very easy to draw far reaching conclusions from correlation data, but immense care should be taken in assigning cause and effect, or even significance to the correlations. The relative faunal similarity of the past two millennia, preceded by a reduction in similarity with the third millennium BP, could be considered to reflect recent human impact on the environment. The Late Bronze Age-Early Iron Age is often considered the starting point for large scale landscape modification, especially in the British Isles (cf. Bell & Walker 2005), where the majority of the beetle data used here are from. However tempting

this may be, the number of samples involved are too few, and a more detailed consideration of chronologies and site locations needs to be employed before this can be further investigated.

Table 6.18. Modified Sørensen (Southwood, 1978) correlation coefficients comparing 1 000 year time slices for the past 20 000 years. Note that the full dataset has been used, and not just the MCR species, and time slices with no data have been omitted.

	00-01K	01-02K	02-03K	03-04K	04-05K	05-06K	06-07K	07-08K	08-09K	09-10K	10-11K	11-12K	12-13K	13-14K	14-15K	18-19K
00-01K																
01-02K	0.49															
02-03K	0.25	0.35														
03-04K	0.11	0.17	0.73													
04-05K	0.27	0.25	0.28	0.27												
05-06K	0.00	0.00	0.00	0.00	0.00											
06-07K	0.14	0.15	0.09	0.06	0.07	0.00										
07-08K	0.15	0.15	0.09	0.07	0.13	0.00	0.44									
08-09K	0.13	0.12	0.08	0.07	0.18	0.00	0.22	0.47								
09-10K	0.10	0.16	0.29	0.22	0.18	0.00	0.03	0.06	0.06							
10-11K	0.09	0.12	0.31	0.23	0.15	0.00	0.03	0.04	0.04	0.39						
11-12K	0.10	0.14	0.31	0.25	0.14	0.00	0.03	0.05	0.05	0.32	0.59					
12-13K	0.15	0.20	0.33	0.27	0.23	0.00	0.06	0.09	0.09	0.37	0.38	0.47				
13-14K	0.11	0.09	0.07	0.06	0.09	0.00	0.08	0.12	0.17	0.05	0.08	0.08	0.12			
14-15K	0.09	0.06	0.03	0.03	0.06	0.00	0.07	0.06	0.10	0.02	0.02	0.02	0.04	0.19		
18-19K	0.01	0.01	0.00	0.01	0.01	0.00	0.06	0.05	0.06	0.00	0.01	0.01	0.01	0.07	0.15	
19-20K	0.01	0.00	0.00	0.00	0.00	0.00	0.02	0.02	0.01	0.00	0.01	0.01	0.01	0.06	0.09	0.21

The similarity between time slices 11-12K and 10-11K is unexpected, as these should, in theory, represent the climatically different Bølling/Allerød (warm) and Younger Dryas (cold) periods respectively. Previous work (e.g. Coope *et al.*, 1998) has shown that, at least in the British Isles, beetles can be used to identify these climatic zones, and as discussed above, it is surprising that they are not easily identified in this study. Even so, the time slices described quite different thermal environments. Of the 695 taxa found in these slices, 277 are common to both, but only 89 of these are in the MCR dataset. It appears that other faunal components than those in the MCR calibration set are more stable than the beetles used to examine climate change. The relatively high coefficient value indicates that climatic difference is no guarantee of a difference in the correlation coefficient. This difference is to be anticipated, as the MCR method and coefficient calculations are mathematically dissimilar, including the fact that the coefficient uses abundance data whereas MCR does not. The coefficient of comparison, when based on raw assemblage data, seems to be of little use in defining climatic zones, even if it may be useful when supporting zones based on the ecology of the beetles (see section 6.2.4). As yet, too little statistical work has been done on fossil beetle faunas to be able to assess the effect of different types and sizes of assemblages on the ability of the coefficient to help in analyses, and more work is necessary on a wide variety of sites and modern data.

There is too little data to be able to investigate the mid-Holocene from this dataset, and the apparently very low similarity between faunas from 6 ka to 3 ka BP is simply a reflection of this. One might expect stability during this period at the millennial resolution, even if large herbivores are active in keeping forest structures periodically open (Vera, 2000).

There is a weak positive relationship (linear regression: $R^2=0.22$) between the value of the coefficient and the number of taxa (in the older of the two time slices compared in each cell). This could be a reflection of bias in either the coefficient or the dataset, and individual sample based analyses should be undertaken to investigate this, along with the application of other coefficients. Faunal stability is an important component in our understanding of past environmental change, and its study could help refine our understanding of how species react to varying degrees of natural, or human induced, habitat loss.

6.7.6 An experiment in large scale environmental reconstruction, and a test of the BugStats %SumRep standardization method

The full time slice dataset, not restricted to MCR taxa, was used to produce an environmental reconstruction using BugStats. This is not an unproblematic undertaking, and it is used here as an experiment to see how the BugStats system responds to such a problem. The geographical range of sites used is relatively large, from a European perspective (Figure 6.26), and so at any one time there will be a number of different large scale environments at the different sites. Beetles may, in many cases, only represent the local environment of a site, and thus general changes in landscape may not be seen by compiling data from multiple sites. In addition, the large time slices mean that the environments of any site may vary considerably within the time slice.

A number of these concerns are equally valid for the temperature reconstruction, but since the reconstruction of habitats includes assumptions based on considerably more variables than temperature, the results of this experiment are less likely to be accurate. The results are not expected to be viable, but are presented here (Figure 6.32) for the sake of experimentation, and as an aid to the discussion of climate-environment interactions, and the use of classification based habitat reconstructions for large scale environmental reconstruction. If anything, the diagrams may show the evolution of the general environment of northern Europe over the last 20 000 years.

The 05-06K timeslice, with only presence values for four taxa from the site Kinfauns, in Scotland, proved to have far too few species to be of use, even with standardization. These four taxa, *Cerylon* spp., *Grynobius planus* (F.), *Anobium* sp., and *Apoderus coryli* (L.) however, all suggest *Wood & trees* with *Dry dead wood* available, but most probably do not account for 100 % of the habitats, as their inclusion in the diagram would have implied. As indicated above, more dated samples are needed from the Early-mid Holocene to be able to answer a number of key questions on the environment of this period.

The *Stored grain pest* chart has been omitted from the diagram (Figure 6.32), due to the slight nature of the signals given by it. Although there are indications of stored grain pests at various points through the data, the majority of these are high level identifications on genera such as *Ptinus*, which are not specific enough to be of use in this large scale reconstruction. Time slice 02-03K includes a number of individuals of *Sitophilus granarius* (L.) from Okruglo in Croatia (Smith *et al.*, 2006), which represent the earliest dated occurrence of the grain weevil in this dataset. The count data for this site is semi-quantitative, which is not ideal for habitat reconstruction, but as abundance weighting is not being used in this particular reconstruction the data are of some use.

There appears to be a peak in woodland indications during the mid Holocene (6 ka to 3 ka BP), with specific indications of deciduous or coniferous woodland at various points. This is in line with existing understanding of the British landscape of this time, from which the majority of samples originate. The lack of data for the period 9 ka to 5 ka BP may obscure the true nature of this peak. There appears to be a greater presence of aquatic habitats in the early Holocene than mid-late Holocene, and the earliest post-Glacial samples (14-15K and 13-14K) suggest a dominance of running water over standing water. This could be interpreted in terms of the release of water from the melting of the remains of the ice masses and permafrost covering the British Isles, which then stabilises in the formation of lakes. These lakes are successively silted up, and give way to the development of more fully vegetated landscapes with time. This hypothesis can be at least partly supported by the similarity of the *Disturbed/arable* signals which should correspond to more mobile, disturbed environments.

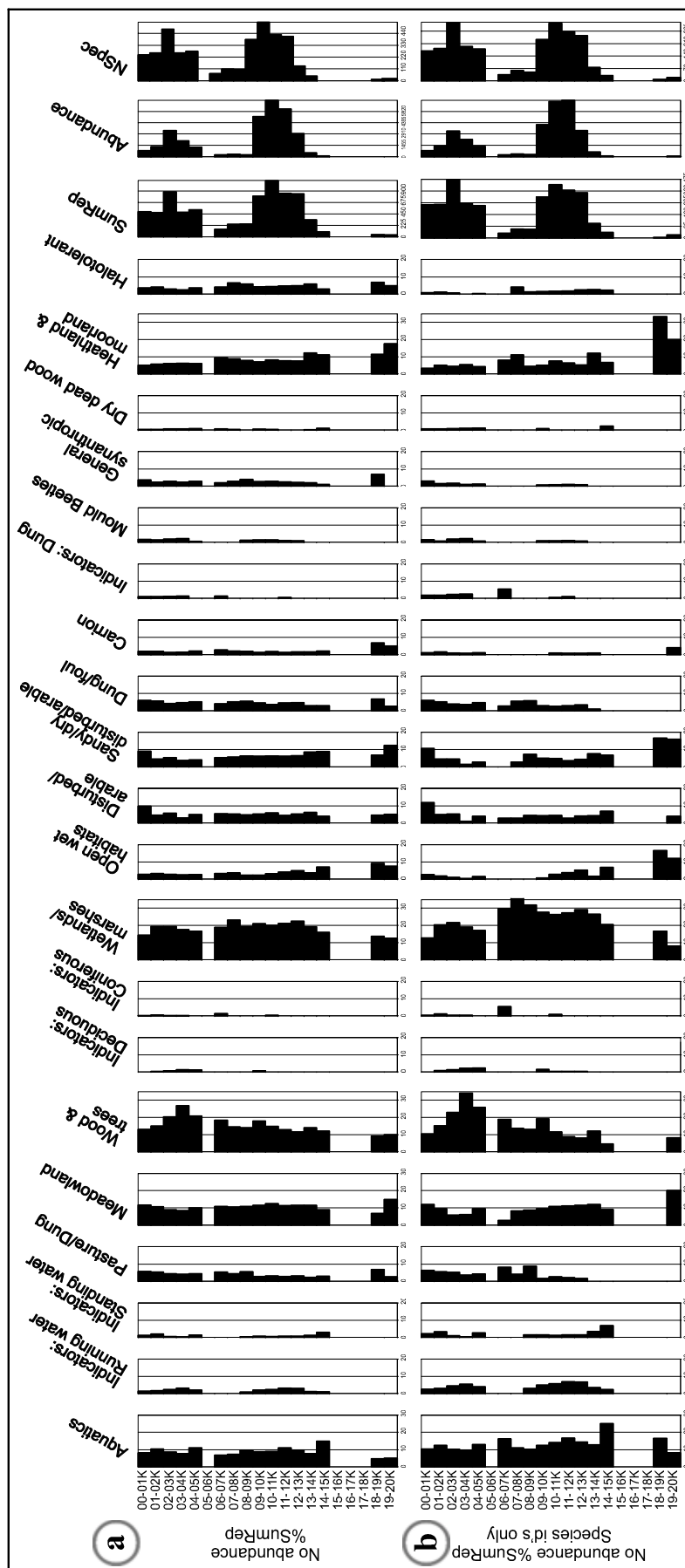


Figure 6.32. BugStats EcoFigs for the last 20 ka in 1 000 year slices, using taxa data only, (a) using all taxa, and (b) species identifications only.

It is possible that the signals in the more general habitat classes (*Aquatics*, *Meadowland*, *Wood & trees*, *Wetland/marshes* and *Heathland & moorland*) are being smoothed by the variety of sites and environments represented in each time slice. If this is so, then the narrower, and indicator, classes may be of more use in describing important characteristics of time slice environments. The lack of woodland indicator species before 11 ka BP is probably a reliable indication of the start of woodland development after the Younger Dryas. The presence of various kinds of dung indications throughout the later part of the timescale, along with openness indications such as *Meadowland* and *Disturbed/arable* habitats could lend support to the Vera hypothesis of openness in mid-Holocene forests (Vera, 2000; Hodder *et al.*, 2005). Further site based research is necessary before this can be evaluated in greater detail, as recommended by Buckland [*et al.*] (2005).

The standardization method used in the production of BugStats EcoFigs was designed specifically to remove the effect of variable numbers of species or individuals between samples. Although not a rigorous test of the success of this method, the calculation of a correlation coefficient of individual habitat class results against either sample number of species or abundance sums should provide an indication as to whether this has been achieved. Only number of taxa have been used in this example (Figure 6.32), although as a relationship has been established between the number of taxa and number of individuals (Figure 6.31b), the results should be similar. If the representation of habitats produced by standardized BugStats outputs was proportional to the number of species, we could expect a correlation between the habitat class values for each sample and the total number of species per sample. As can be seen from Table 6.19, the raw, untransformed values generally display this relationship (higher R^2 values), with the exception of a few categories which have very low counts. Standardization lowers the correlation significantly in all but a few cases, suggesting that the standardization method successfully counters the affect of varying sample sizes.

A similar effect can be seen when log transformations are applied to the raw data and sums, although the effect is less pronounced in most cases, and even appears to have little effect in the case of the *Standing water* and *Mould beetle* habitats. The significance of this is difficult to interpret, and although the transformation option is not recommended, it may be introducing additional artefacts into the equation due to biases in the coding system.

Table 6.19. The effect of standardization (Std) on the relationship between *sample habitat sums* and *the numbers of species in samples* (species level identifications only). Values are R^2 , the Pearson product moment correlation coefficient, indicating the proportion of the variance in the habitat class values that is attributable to variance in the numbers of species. Values are shaded by magnitude, and a higher value indicates greater correlation.

		Aquatics	Indicators: Standing water	Indicators: Running water	Pasture/Dung	Meadowland	Wood and trees	Indicators: Deciduous	Indicators: Coniferous	Wetlands/marshes	Open wet habitats	Disturbed/arable	Sandy/dry disturbed/arable	Dung/foul habitats	Carriion	Indicators: Dung	Mould beetles	General synanthropic	Dry dead wood	Heathland & moorland	Halotolerant
No transformation																					
NSpec	Raw	0.94	0.90	0.54	0.61	0.88	0.67	0.39	0.27	0.94	0.52	0.63	0.67	0.81	0.71	0.37	0.75	0.66	0.27	0.89	0.59
	Std	0.13	0.79	0.03	0.08	0.18	0.31	0.29	0.00	0.23	0.02	0.17	0.00	0.28	0.04	0.04	0.67	0.49	0.05	0.03	0.07
Ln transformed NSpec and habitat values (Transform abundance Ln(n+1) option in BugStats)																					
NSpec	Raw	0.96	0.72	0.63	0.68	0.90	0.89	0.38	0.20	0.96	0.53	0.81	0.79	0.77	0.52	0.30	0.57	0.56	0.28	0.94	0.57
	Std	0.29	0.70	0.40	0.42	0.46	0.58	0.36	0.07	0.32	0.03	0.67	0.11	0.63	0.30	0.18	0.57	0.57	0.21	0.05	0.38

6.7.6.1 Relationships between reconstructed temperatures and habitats

In the Koivula *et al.* (2004) case study above (section 6.1.6), a slightly wider span of temperature reconstructions were obtained from the forest habitat than the from the farmland fauna. It was therefore suggested that there may be a relationship between the habitats of the species used in temperature reconstructions and the MCR values obtained from them, which might lead to slightly different temperature reconstructions within a region. This could mean that if the dominant habitat of the area represented by a sequence of samples changes with time, then the temperatures reconstructed from different samples could under- or overestimate periods of the past climate. This could be considered, to a certain degree, to relate to the scepticism expressed by Andersen (1993) on the validity of the MCR method. Although the MCR method has been validated with modern data (Atkinson *et al.*, 1987; Coope & Lemdahl, 1996), this has not been done in combination with quantitative reconstruction of the habitats represented by the faunas. The 20 ka dataset was used to test whether any such relationships, between the reconstructed temperatures and the strength of the habitat signals from species level identifications (Figure 6.32b), could be identified for the past 20 000 years using the bulked 1 000 year time slices. Linear regression was used, and although this is not a particularly robust test, or a thorough analysis of the potential relationships, it may allow us to assess the relative amount of variability in each habitat group that can be linearly related to the reconstructed temperatures. Due to the broad nature of the dataset, it may be unwise to attempt more thorough analyses than those presented here, and a more rigorous, site by site analysis would most likely prove more fruitful should this experiment be taken further. The R^2 values for the regression of each habitat group with each reconstructed temperature variable (TValues) are presented in Table 6.20. The strength of the relationships are not given, as the author does not believe that the results would have any ecological grounding in this case, but the direction of the relationship is indicated by the underlining of negative trends. Note that these results do not in any way imply cause and effect, which is liable to be a complex issue, but could form the starting point for further investigations into the relationship between reconstructed habitats and temperatures.

Were the pattern seen in the results from the Koivula *et al.* (2004) data common to the 20 ka dataset, then one would perhaps expect to see a large part of the variation in either the *Wood & trees*, *Sandy/dry disturbed/arable* and/or possibly *Disturbed/arable* habitat groups ‘explained’ by the TMaxDiff and TMinDiff variables. These are the habitat groups that displayed the largest signal differences in the BugStats results for the Koivula *et al.* data (see Figure 6.3), and are thus most likely to be those responding to forest/grassland differences in that context. The low R^2 values for each of these (highlighted in **bold** in Table 6.20) suggest that the pattern is not reproduced in the 20 ka time slices. There are, however, a number of more significant correlations, the most prominent being *Open wet habitats*, *Sandy/dry disturbed/arable* and *Heathland & moorland* (independently) with TMax and TMin. As might be expected, these suggest that these types of environment are more frequent during colder periods. In addition, *Dung/fowl habitats* appear to be correlated with TMax and to a lesser extent TMinII. This could, at least theoretically, be explained in terms of warmer summer temperatures leading to generally higher numbers of herbivores, in a complex relationship involving biological productivity and the ability of the environment to support more large vertebrates (e.g. Brown & Lomolino, 1998).

It should be remembered that only a subset of the species used for habitat reconstruction are used for climate reconstruction, and one should perhaps, ideally, run BugStats on just the MCR species to reduce the risk of coincidental patterns. As mentioned above, the 20 ka dataset only allows the investigation of geographically and chronologically broad scale changes, and the differential representation of environments in the time slices makes the interpretation of statistics difficult. The simple analyses presented here, however, demonstrate that the use of the BugStats system together with an enhanced MCR facility may be extremely useful in increasing our understanding of not only past environmental and climate change, but also the biogeography and ecology of insect populations in general.

Table 6.20. Amount of variance per habitat group explained by the different temperature values output from BugsMCR. Cell values are R^2 , and underlined numbers indicate negative relationships. TMaxDiff and TMinDiff are the TMax and TMin spans respectively (e.g. TMaxHi-TMaxLo). Cells are shaded by R^2 value, see the text for explanation of the **bold** highlighted cells.

TValue	Aquatics	Indicators: Standing water	Indicators: Running water	Pasture/Dung	Meadowland	Wood and trees	Indicators: Deciduous	Indicators: Coniferous	Wetlands/marshes	Open wet habitats	Disturbed/arable	Sandy/dry disturbed/arable	Dung/foul habitats	Carion	Indicators: Dung	Mould beetles	General synanthropic	Stored grain pest	Dry dead wood	Heathland & moorland	Halotolerant
TMaxLo	<u>0.09</u>	0.42	0.01	0.20	0.00	0.27	0.17	<u>0.03</u>	0.19	<u>0.66</u>	0.07	<u>0.45</u>	0.60	<u>0.07</u>	0.00	0.34	0.30	0.07	0.01	<u>0.66</u>	0.14
TMaxHi	<u>0.13</u>	0.32	<u>0.00</u>	0.33	<u>0.01</u>	0.29	0.15	<u>0.00</u>	0.19	<u>0.64</u>	0.04	<u>0.46</u>	0.75	<u>0.08</u>	0.02	0.32	0.31	0.04	0.00	<u>0.57</u>	0.08
TMinLo	<u>0.03</u>	0.37	0.11	0.02	0.14	0.34	0.24	<u>0.01</u>	0.03	<u>0.55</u>	0.16	<u>0.43</u>	0.18	0.01	0.00	0.31	0.21	0.06	0.17	<u>0.77</u>	0.09
TMinHi	<u>0.03</u>	0.13	0.01	0.34	<u>0.08</u>	0.58	0.45	0.03	0.07	<u>0.59</u>	0.02	<u>0.55</u>	0.51	<u>0.16</u>	0.09	0.25	0.18	0.01	0.15	<u>0.55</u>	0.00
TRangeLo	<u>0.00</u>	0.01	<u>0.01</u>	<u>0.08</u>	0.09	0.37	<u>0.36</u>	<u>0.10</u>	0.00	0.11	0.00	0.17	<u>0.03</u>	0.06	<u>0.07</u>	<u>0.02</u>	<u>0.00</u>	0.00	<u>0.32</u>	0.11	0.09
TRangeHi	0.00	<u>0.23</u>	<u>0.19</u>	0.00	<u>0.22</u>	<u>0.27</u>	<u>0.23</u>	0.01	0.00	0.30	<u>0.17</u>	<u>0.25</u>	<u>0.02</u>	<u>0.05</u>	<u>0.00</u>	<u>0.21</u>	<u>0.11</u>	0.04	<u>0.32</u>	0.55	<u>0.03</u>
TMaxDiff	<u>0.01</u>	<u>0.27</u>	<u>0.27</u>	0.11	<u>0.16</u>	0.01	<u>0.03</u>	0.25	<u>0.01</u>	0.08	0.10	0.03	0.01	<u>0.00</u>	0.11	<u>0.07</u>	<u>0.02</u>	<u>0.11</u>	<u>0.16</u>	0.19	<u>0.18</u>
TMinDiff	0.01	<u>0.26</u>	<u>0.13</u>	0.05	<u>0.47</u>	0.03	<u>0.02</u>	0.08	<u>0.00</u>	0.15	0.16	0.09	<u>0.00</u>	<u>0.14</u>	0.02	<u>0.12</u>	<u>0.07</u>	0.06	0.06	0.32	<u>0.15</u>

6.7.7 Conclusions

The application of spatial statistics, or geostatistics, to time slices extracted from BugsCEP data would require careful time-depth modelling of each site to be of real research value. The time slices used in here are simply bulked date categories, with limited regard for the errors involved, and no attempt to interpolate or extrapolate sample dates through sequences. To do so without specific reference to the original publications would be risky to say the least. This has important consequences for the reconstructions in that they should be regarded as extremely tenuous conclusions at best. In reality, some of the inferences drawn may have been misleading due to dating issues. Palaeoenvironmental science is not unique in being subject to these problems, and indeed practically any work which attempts to utilize data from a large spatial and chronological span, both in terms of sample dates and when the research was undertaken, will have similar problems.

Although the examples above use artificially compounded assemblages, they serve to illustrate how careful examination of the jackknifed results, along with the climate space maps for a sample, can help resolve difficulties in the interpretation of MCR climate reconstructions. The use of BugStats illustrates that, although the interpretation of samples which enclose varying environments, either by virtue of their resolution/size, or in this case geographical extension, is problematic, the tools offered by BugsCEP can help considerably. The standardization method (%SumRep) employed in the construction of EcoFigs appears to perform well in this situation, and effectively compensates for the variations in species numbers that are common in sequences of palaeoentomological samples. Further testing, however, at the site level, with both modern and fossil assemblages is required to further validate the method.

